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Lauri Niemistö, Ilkka Rinne, Terttu Melvasalo
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Merentutkimuslaitos
PL 33
00931 Helsinki

Havsforskningsinstitutet
PB 33
00931 Helsingfors

Finnish Institute of Marine Research
P.O. Box 33
SF-00931 Helsinki Finland

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BLUE-GREEN ALGAE AND THEIR NITROGEN FIXATION IN THE BALTIC SEA IN 1980, 1982 AND 1984

Lauri Niemistö[1], Ilkka Rinne[2], Terttu Melvasalo[3] and Åke Niemi[4]

ABSTRACT

The results of studies on the occurrence of heterocystic blue-green algae and their nitrogen fixation in the Baltic Proper and the Gulf of Finland in late July - early August 1980, 1982 and 1984 are reported. Transects from the inner Gulf of Finland to the Gotland Basin, and in 1982 even down to the southwestern Baltic, were investigated. Anchor station studies were carried out in the northern Baltic Proper in 1980 and 1984, and in the southwestern Baltic in 1982. Species distribution and acetylene reduction at different depths were studied.

The late summer blooms were caused by Nodularia spumigena Mert. At the same time Aphanizomenon flos-aquae (L.) Ralfs was more evenly distributed in the water column or reached a maximum in the lower part of the euphotic layer. The dominance of Nodularia increased toward the southern Baltic during this season. Comparison of in situ and in vitro measurements of acetylene reduction showed similar results. The anchor station studies showed that the short-time dynamics of blue-green algal occurrence were not mirrored in the changes in the level of inorganic nutrients in the euphotic layer. The rise of algae to the very surface caused a corresponding increase in the total phosphorus and nitrogen contents.

The studied blue-green algal biomass and nitrogen fixation level fluctuated strongly in space and time owing to patchiness and movement of the water masses, thus causing problems in estimating the total nitrogen fixation in the study area. The daily nitrogen fixation rates in situ varied from 5 - 33 mg N/m^2. The amount of nitrogen fixed in different subareas was estimated at 38 - 2600 kg N/km^2. Compared to earlier studies (1974-1979), no additional evidence concerning trends in the annual intensity of the blooms and nitrogen fixation was found.

Key words: heterocystic blue-green algae, nitrogen fixation, Baltic Sea

1. INTRODUCTION

The mass occurrence and blooms of blue-green algae are typical phenomena in the summer and early autumn in the Baltic Sea, and are caused by nitrogen-fixing species, chiefly *Nodularia spumigena* Mert. and *Aphanizomenon flos-aquae* (L.) Ralfs. The bloom and nitrogen fixation, as well as their horizontal and vertical distribution have been studied as part of the Merininni project since the 1970s (Rinne et al. 1976, 1978, 1979, 1980; Melvasalo et al. 1982, 1983, Melvasalo & Niemi 1985, Niemi 1979, 1982). The amount of nitrogen fixed by these blue-green algae plays an important role in the nitrogen budget of the Baltic Sea (Rinne et al. 1978, Melvasalo et al. 1983, Rönner 1983, Larsson et al. 1985).

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1 Finnish Insitute of Marine Research, P.O. Box 33, SF-00931 Helsinki
2 Helsinki City Water and Sewage Works, Water Conservation Laboratory, Kyläsaarenkatu 10, SF-00550 Helsinki
3 Karhusuontie 21-25, SF-00720 Helsinki
4 Helsinki University, Tvärminne Zoological Station, SF-10900 Hanko

In the anoxic basins of the Baltic Sea, inorganic combined nitrogen is reduced to molecular nitrogen and disappears from the nitrogen store (Sen Gupta 1973, Fonselius 1978, Rönner 1983). As a result, the N:P ratios in the deep basins decrease (Fonselius 1976, 1978). Short-term, wind-generated upwelling and the general circulation pattern result in deep water with a low N:P ratio being gradually transported to the surface to meet the nutrient requirements of the phytoplankton. During the vernal high production of phytoplankton, inorganic phosphorus and nitrogen decrease in the mixed surface layer down to very low concentrations, although some phosphorus remains available (Hobro et al. 1975, Niemi 1975). The lack of inorganic nitrogen and surplus of phosphorus favour the production of nitrogen-fixing, blue-green algae during the summer (Niemi 1979, Horne and Galat 1985).

Although the results from the cruises carried out in the years 1974-1984 showed how difficult it is to make reliable measurements of such a patchy phenomenon as the blue-green algal blooms, emphasis has been laid on the follow-up of the year-to-year variability and possible trends taking place over the years.

The present study is a report of the cruises made from late July to early August in 1980, 1982 and 1984. The study was performed on board R/V Aranda as transect cruises from the eastern part of the Gulf of Finland to the Gotland Deep, and in 1982 also to the southwestern Baltic Sea and in addition three anchor stations were studied.

2. STUDY AREA, MATERIAL AND METHODS

The sampling was performed on board R/V Aranda, the research vessel of the Finnish Institute of Marine Research. The transects and the location of the anchor stations are presented in Fig. 1 and Table 1.

Hydrographic and chemical analyses were made on board using the Institute's standard methods (Grasshoff 1976, Koroleff 1976, 1979). Chlorophyll *a* was measured using the fluorometric method (Lorenzen 1966). The blue-green algae and the number of heterocysts were counted from concentrated net (20 μm) samples (taken from depths of 0, 5, 10, 15 and 20 m, at anchor stations additionally from 2.5 m), preserved in Keefe's solution and counted using the Utermöhl technique (see Melvasalo et al. 1973 for details of the counting method).

Nitrogen fixation was measured from the same concentrated samples as the phytoplankton using the acetylene reduction method (Burris 1972). Our application is described in detail in Vuorio (1977), Vuorio et al. (1978) and Rinne et al. (1978, 1979). During the transect cruises nitrogen fixation was measured *in vitro* and at the anchor stations additionally *in situ*.

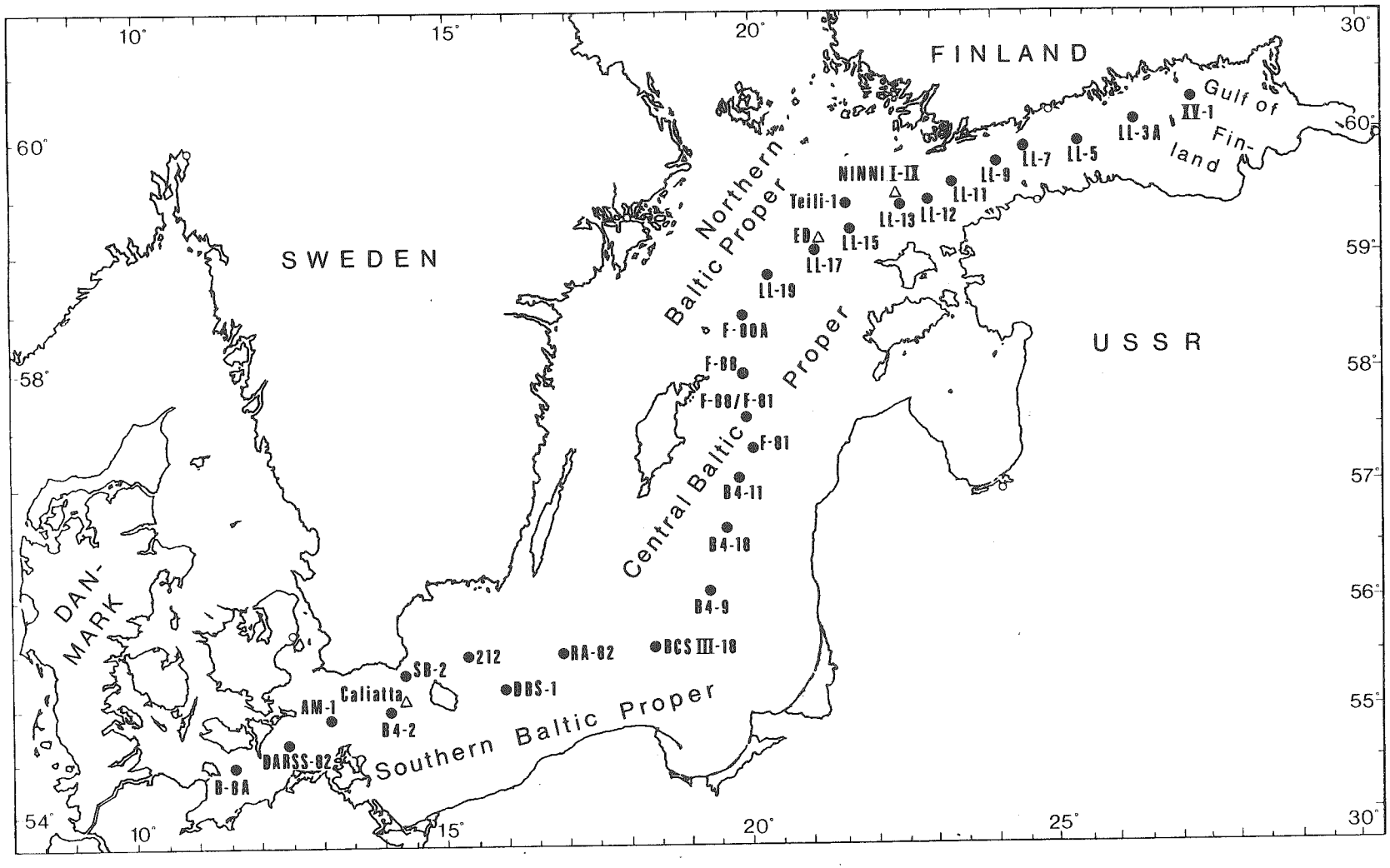

Fig. 1. Study area and sampling stations (cf. Table 1).

TABLE 1. Sampling stations, their coordinates and depths.

Area	Stations	Coordinates		Max. depth m
Gulf of Finland	XV-1	60°15',	27°15.0'	68
	LL-3a	60°04.4'	26°20.5'	65
	LL-5	59°55.0'	25°26.0'	69
	LL-7	59°51'	24°50'	80
	LL-9	59°42'	24°02'	65
	LL-11	59°35'	23°18'	67
	LL-12	59°29'	22°54'	82
Northern Baltic Proper	LL-13	59°22'	22°28'	100
	Ninni I-IX*	59°30'	22°23.5' *	67
	Ninni Bloom	59°16.5'	21°47.1'	120
	LL-15	59°11'	21°45'	126
	LL-17	59°02'	21°05'	164
	Teili 1	59°26.5'	21°32'	164
	ED	59°08.5'	21°12.7'	139
Central Baltic Proper	LL-19	58°53'	20°19'	170
	F-80a	58°30'	19°50.2	175
	F-80	58°00'	19°54'	185
	F-80/81	57°40'	19°58'	126
	F-81	57°19'	20°02'	234
	BY-11	57°04'	19°50'	214
	BY-10	56°38'	19°35'	143
	BY-9	56°07'	19°18'	112
Southern Baltic Proper	BCSIII-10	55°33'	18°24'	89
	DBS-1	55°15'	15°59'	86
	212	55°29'	15°19'	83
	SB-2	55°20'	14°21'	53
	Caliatta	55°02'	14°19'	43
	BY-2	55°00'	14°05'	47
	RA-82	55°29'	17°56.0'	68
	AM-1	54°52'	13°06'	42
	DARS-82	54°43.5'	12°28'	19
	B-8a	54°29.4'	11°32.8'	25

* A drifting station, starting coordinates

3. TRANSECT CRUISES

3.1 Hydrographic-chemical conditions

The hydrographic conditions were quite similar in late July - early August in all the study years (Figs. 2, 3, 4). The thermocline at a depth of 10 - 20 m separated the mixed surface layer, where temperatures above 15 °C were prevailing (about 20 °C in the southern Baltic in 1982). The winter water layer at a depth of 40-50 m was well discernible. Anoxic conditions occurred in the deeps. The permanent halocline occurred at 60 - 80 m, rising upwards in the southwestern Baltic Sea, and becoming less discernible in the inner Gulf of Finland. The salinity of the mixed surface layer gradually increased from below 5 °/oo in the inner Gulf of Finland to c. 7 °/oo in the central Baltic Proper, and 8 °/oo in the southwestern Baltic Sea. The pH in the euphotic layer rose during the production stage to above 8.5 throughout almost the whole study area. Thus the cruises described here were made under periods of hydrographically stable summer conditions.

During this season, characterized by a well developed thermic stratification, the concentrations of all inorganic nutrients in the euphotic layer were relatively high at the easternmost station XV-1 in 1982, where the nutrient concentrations were higher owing probably to a eutrophying influence from the eastern Gulf of Finland.

The phosphate concentrations in the mixed surface layer were somewhat higher in the Gotland Deep area in 1980 and 1982 than in the other areas studied. The total phosphorus level varied between 0.3 and 0.5 μmol l^{-1}. In 1982 some higher values were measured at the entrance to the Gulf of Finland and east of Bornholm. In the stagnant bottom water the maximum concentration of phosphorus (μmol l^{-1}) increased, following the continuation of the stagnation from 4.0 (1980) to 4.4 (1982) and to 5.1 (1984).

The mixed surface layer was depleted of inorganic combined nitrogen, except for the Gulf of Finland where some higher NH_4 concentrations were measured. Higher ammonium concentrations occurred sporadically above the maximum nitrate layer. The vertical nitrite maximum occurred above the permanent halocline. In the open Baltic Proper the vertical nitrate maximum occurred at a depth of 70-100 m, in the Gulf of Finland at 40-70 m. In the anoxic deeps the inorganic nitrogen occurred as ammonium, reaching the highest values (> 22 μmol l^{-1}) in the Gotland Basin 1984.

The lowest concentrations of total nitrogen in the surface water were found in the Gotland Deep area. The concentrations increased towards the inner Gulf of Finland. Concentrations markedly above 20 μmol l^{-1} were measured in 1982 also in the Bornholm area. In 1982 a vertical minimum was observed in the central basin at a depth of 100 - 150 m. However, it had disappeared in 1984 when a maximum > 35 μmol l^{-1} had developed near the bottom.

The distribution of chlorophyll *a* showed a very complicated patchy distribution system in 1982 (Fig. 6), with local maxima in different areas and

different depths. The lowest concentrations were observed in the Gotland Deep area.

The nutrient conditions did not differ very much during the three transect studies. The levels of total nutrients were about the same. The small differences in inorganic nutrients in the surface layer were probably a result of different stages of phytoplankton dynamics.

3.2 Blue-green algae and nitrogen fixation

Aphanizomenon flos-aquae and *Nodularia spumigena* were the dominant heterocystic blue-green algae throughout the transects (Figs. 5, 6, 7, 8). A clear difference in the vertical maximum occurrence of these species was observed. *Nodularia* was found abundantly in the uppermost 5 metres (Figs. 9, 10), while *Aphanizomenon* was distributed throughout the euphotic layer and had a vertical maximum at various depths.

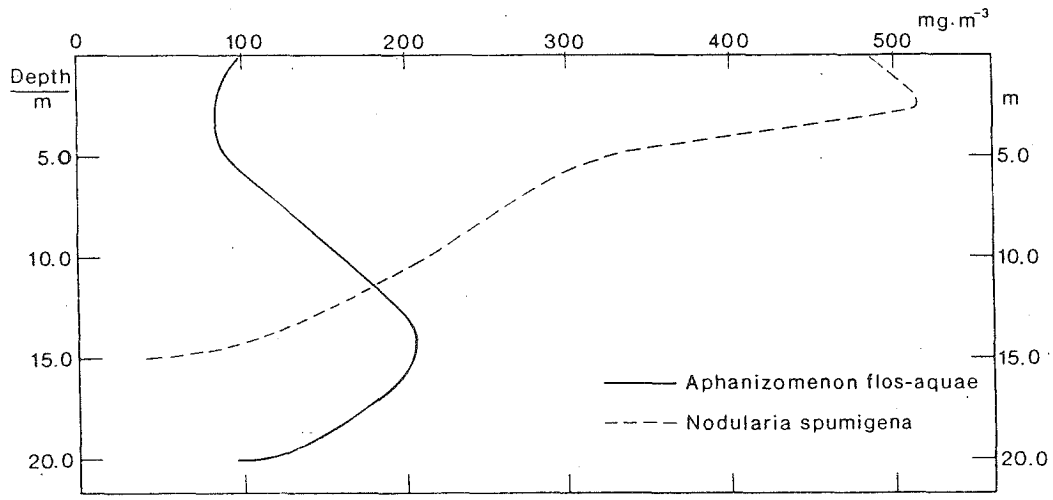

Fig. 9. Vertical distribution (mg · m^{-3}) of Nodularia spumigena (dotted line) and Aphanizomenon flos-aquae (solid line) at station Ninni Bloom in August 1984.

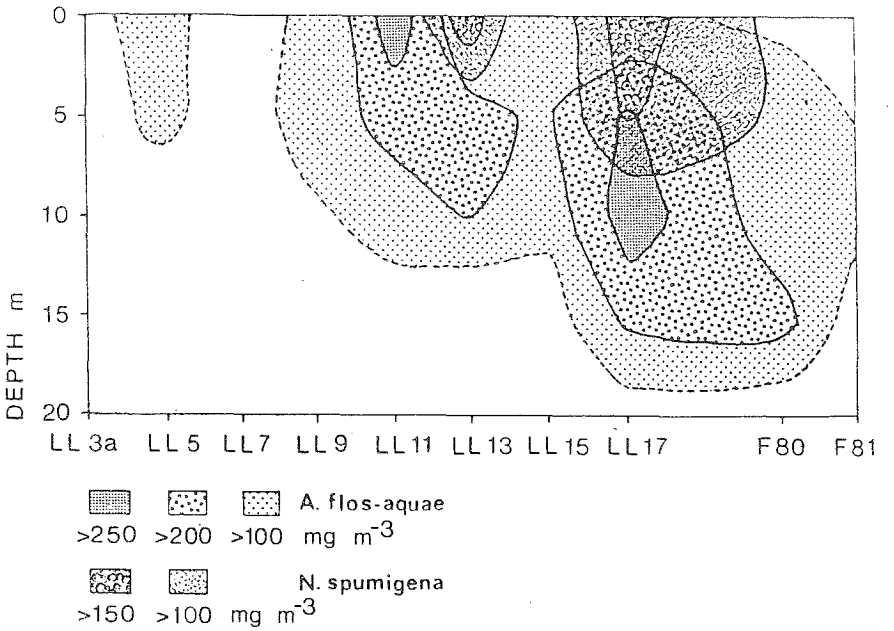

Fig. 10. General presentation of the occurrences of Nodularia spumigena and Aphanizomenon flos-aquae on the transect LL-3a - F-81, July 27 - 30, 1980.

Nodularia was of greater importance in the Southern Baltic, whereas the proportion of *Aphanizomenon* (Table 2) decreased towards the southern part of the Baltic Sea. The proportion of *Anabaena* was small throughout the whole area.

TABLE 2. Percentages of Aphanizomenon flos-aquae, Nodularia spumigena and Anabaena spp. out of the total biomass of heterocystic blue-green algae per square metre (0-20 m) in 1980, 1982 and 1984 in different subareas of the Baltic Sea.

Area	Species	1980	1982	1984
Gulf of Finland	Aphanizomenon	92	92	74
	Nodularia	4	7	25
	Anabaena	4	1	1
Northern Baltic Proper	Aphanizomenon	78	54	34
	Nodularia	18	44	66
	Anabaena	4	2	0
Central Baltic Proper	Aphanizomenon	70	20	24
	Nodularia	26	73	75
	Anabaena	5	7	1
Southern Baltic Proper	Aphanizomenon		9	
	Nodularia		81	
	Anabaena		10	

In 1980 the greatest abundances were found in the northern Baltic Proper and at the entrance to the Gulf of Finland but in 1984 they occurred in the central Baltic proper (Figs. 11, 12, 13). In 1982 the strongest blooms were encountered in the southern and southwestern Baltic Proper.

The number of heterocysts correlated well with the biomass of heterocystic algae. *Aphanizomenon* had c. 2 heterocysts per mm of filament, *Nodularia* c. 18 and *Anabaena* c. 1, respectively.

The heterocystic activity in the samples from the depths of 0 - 5 m was of the same order of magnitude in the northern and central Baltic Proper and in the Gulf of Finland (0.14 - 0.46 pMC_2H_2 (red.) (2 h. het.)$^{-1}$)* in 1980 and in 1982. In the southern part of the Baltic Sea greater activities were measured in 1982. In 1984 the activity in the Gulf of Finland and in the northern Baltic Proper was markedly higher, varying from 0.57 to 1.85 pM het^{-1} (2 h)$^{-1}$ and in the central Baltic Proper from 0.4 to 0.92. The acetylene reduction rate and these values converted to nitrogen fixation values are presented in Table 3.

TABLE 3. The acetylene reduction rate (μmol C_2H_2 (red.) m^{-2} (1 h)$^{-1}$**) and calculated nitrogen fixation values (μg N (2 h)$^{-1}$ m^{-2}) in different subareas during the study years.

	Acetylene red. rate	Nitrogen fixation
Gulf of Finland	1980	18 - 184	170 - 1700
	1982	6 - 12	60 - 110
	1984	84 - 145	780 - 1400
Northern Baltic Proper	1980	50 - 300	470 - 2800
	1982	18 - 77	170 - 720
	1984	490 - 790	4600 - 7400
Central Baltic Proper	1980	120 - 218	1100 - 2000
	1982	45 - 185	420 - 1700
	1984	103 - 580	960 - 5400
Southern Baltic Proper	1982	51 - 260	480 - 2400

Mean nitrogen fixation values have been calculated for the whole growing period (Table 4), assuming that the seasonal, diurnal and vertical variations in the nitrogen fixation do not differ from those off the Helsinki area (Vuorio 1977, Vuorio et al. 1978).

* Pico moles acetylene reduced per heterocyst in two hours.

** Micro mole acetylene reduced per square meter per hour.

TABLE 4. Calculated nitrogen fixation (kg N · km^{-2}) during the growing period in different subareas and study years. The calculations were based on the assumption that about 2 % of the nitrogen fixed during June - August is fixed during one single day in late July or in early August; the surface (0 m) fixation is c. 12 % of that in the whole water column (0 - 22.5 m); the fixation in one hour in late July or early August corresponds to 2 - 7 % of the daily fixation depending on during which time of the day the measurements are made.

	Year	kg N · km^{-2}
Gulf of Finland	1980	170
	1982	38
	1984	490
Northern Baltic Proper	1980	700
	1982	130
	1984	2600
Central Baltic Proper	1980	380
	1982	430
	1984	780
Southern Baltic Proper	1982	440

4. ANCHOR STATIONS

4.1 Station ED, 1980, July 27 - 30

Hydrographic-chemical conditions. The initial (July 27) surface water jtemperature, 17.4 °C, increased by c. 2 °C during the study period. The thermocline was not very sharp and the salinity varied very little during the study period (Fig. 14). The concentration of inorganic phosphorus was, in general, less than 0.1 μmol l^{-1} in the euphotic layer, but increased rapidly with depth. On July 29 and 30 the phosphate concentrations increased somewhat on the surface. In the euphotic layer PO_4-P comprised about 20 % of the total phosphorus. The fluctuations in nutrient concentrations, especially those of ammonium-nitrogen, could not be directly connected with the dynamics of the blue-green algal biomass in the water column during the anchoring period. Fluctuations in salinity point to changing water masses during the anchoring period.

Blue-green algae and nitrogen fixation. The biomass and the number of heterocysts of *Aphanizomenon* were dispersed down the water column compared with that of *Nodularia* and *Anabaena* (Fig. 15). The maximum of *Aphanizomenon* was at a depth of 10 - 15 m. The maximum occurrence of *Nodularia* and *Anabaena* was near the surface. During the last stage of the bloom, *Nodularia* could be observed as large strips unevenly distributed on the water surface throughout the area. The species composition of the bloom was very stable throughout the period, *Aphanizomenon* accounting for about 67 % of the biomass of blue-green algae and *Nodularia* and *Anabaena* for 30 % and 3 %, respectively. The highest heterocystic activity values were found near

the surface during daytime (Fig. 16). The acetylene measurements per area *in vitro* and *in situ* were in good correlation (r = 0.91, d.f. = 13) with each other, and the *in situ* values per area were about 0.71 (sd = 0.10, d.f. = 10) times the *in vitro* results during the daytime. The ratio in the surface layer (0 m samples) was 0.88 (sd = 0.18, d.f. = 10).

The daily nitrogen fixation rate can be calculated from the *in situ* measurements as follows:

July 27	19	mg N_2 m^{-2} d^{-1}
July 28	14	- " -
July 29	24	- " -
July 30	33	- " -

Nitrogen fixation during the growing period was estimated to be c. 1000 kg N_2 km^{-2} in the anchor station area using the assumption concerning seasonal variations presented in Table 4. The corresponding calculation based on surface layer (0 m samples), *in vitro* measurements gave 1100 kg N_2 km^{-2} (assumptions in Table 4). This is in good accordance with the *in situ* results.

4.2 Station Caliatta, 1982, August 3 - 4

Hydrographic-chemical conditions. The surface water temperature was over 20 °C. The thermocline occurred at a depth of 10-15 m (Fig. 17). No changes in salinity were observed during the anchoring period. The concentration of total phosphorus remained almost constant, the inorganic phosphorus in general being less than 0.05 μmol l^{-1} in the eutrophic layer. Ammonium levels varied somewhat, showing a diurnal maximum before noon. However, the chemical and hydrographical conditions were quite stable during the anchoring study period. The higher total nitrogen values recorded in the surface coincided with the blue-green algal biomass values.

Blue-green algae and nitrogen fixation. *Nodularia* dominated the blue-green algal biomass and occurred in the upper part of the euphotic layer. *Aphanizomenon* and *Anabaena* spp. were of minor importance (Fig. 18). Their occurrence expressed as a percentage was 87, 12 and 1 %, respectively. During the study period the biomass of *Nodularia* fluctuated between 1000 and 6300 mg m^{-2}, showing an increasing trend during the period.

The acetylene reduction rate results per area *in vitro* and *in situ* showed good correlation (r = 0.98, d.f. = 4) with each other, and the *in situ* value per area was 1.3 (sd = 0.20, d.f. = 5) times the *in vitro* result. The ratio was also 1.3 (sd = 0.09, d.f. = 5) in the surface layer (0 m samples) . Below the depth of 10 m the amount of blue-green algae and acetylene reduction was negligible. The daily fixation rate amounted to 7 mg N_2 m^{-2}.

4.3 Station Ninni, 1984, July 30 - August 1

Hydrographic-chemical conditions. The surface temperature increased by 1 °C during the period. The thermocline occurred at a depth of 5 - 15 m (Fig. 19). The level of inorganic nutrients was low throughout the anchoring period. The nature of the water column changed on the second study day (at 14.30 o'clock), probably as a result of a change in the water mass. A high level of total phosphorus, total nitrogen and pH in the surface water at the beginning of the period coincided with a greater abundance of blue-green algae.

Blue-green algae and nitrogen fixation. The blue-green algal biomass consisted of *Aphanizomenon* and *Nodularia*, the latter dominating and showing greater fluctuations, 50 - 200 $\mu g \cdot l^{-1}$ (Fig. 20). The bloom declined towards the end of the anchoring period, probably owing to changing water masses.

The acetylene reduction rate fluctuated, varying between 30 - 330 $\mu mol\ m^{-2}\ (2\ h)^{-1}$. The correlation coefficient between the *in vitro* and *in situ* values per area was 0.99 (d.f. = 7) and highly significant, and the *in situ* results per area were 0.72 (sd = 0.12, d.f. = 8) times the *in vitro* results. The ratio in the surface layer was 1.0 (sd = 0.08, d.f. = 8). The daily rates of nitrogen fixation were calculated to be 22 and 5 mg N m^{-2}. A large amount of blue-green algae and a high nitrogen fixation were found in the uppermost 5 m layer.

A case study (st. Ninni-bloom) carried out after the anchoring station period showed a heavy bloom of *Nodularia*, while at the same time *Aphanizomenon* had developed a maximum at the depth of 15 m (Fig. 9).

4.4 General views on the anchor station studies

The three anchor station studies were characterized by stable, fair weather. The anchoring periods were, however, too short to make sophisticated observations possible on the development of a bloom. Only short dynamic stages could be studied.

No clear connection was found between the development of a bloom and the concentrations of inorganic nutrients during the anchor station studies. However, the rising of the algae up to the surface could be observed as increased concentrations of total phosphorus and nitrogen on the surface. This probably reflects the combined effect of transportation and the discharge of phosphorus from the decaying cells.

The great variations in the inorganic N:P ratio (Table 5) were due to the fact that the analysis values lie near the lower detection limit. However, the low N:P ratios in the euphotic layer at the Ninni station are remarkable.

TABLE 5. Inorganic molar N:P ratio ((NO3 + NH4) - N/PO4-P) at anchor stations ED, Caliatta and Ninni.

Depth m	ED, 1980 inorg. N:P			Caliatta, 1982 inorg. N:P			Ninni, 1984 inorg. N:P		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
0	9.7	7.4	17	7.6	9.7	4	2.6	2.9	7
5	12.9	11.7	17	4.5	5.9	4	1.6	1.4	7
10	11.9	11.0	17	5.2	2.8	4	1.2	1.2	7
15	10.7	12.3	17	1.9	0.9	4	0.3	0.2	7
20	6.2	4.5	17	0.5	0.2	4	1.1	0.9	7
30	1.9	1.3	17	0.1	0.2	4	3.3	2.0	7
40	2.0	1.0	17	3.2	0.5	4	4.4	1.5	7
50							5.1	0.2	2
60	2.8	2.1	4				5.2	0.0	2
80	3.0	1.1	5						
100	0.8	0.4	5						

The amount of the daily nitrogen fixation per area fluctuated markedly along the varying amounts of blue-green algae (5 - 33 mg N_2 m^{-2}). This again is connected to patchiness and the moving water masses. The *in vitro* measurements of nitrogen fixation were fully comparable to the *in situ* results.

The different ecology of the two main species was also apparent at the anchor stations. When *Nodularia spumigena* developed a biomass maximum at the surface, *Aphanizomenon flos-aquae* was in some cases found to be most abundant in the lower part of the euphotic layer, in the thermocline layer. The biomass of *Nodularia* showed markedly greater variations in space and time than *Aphanizomenon*.

5. DISCUSSION

Hydrographic and chemical factors and the blooms. The ammonia concentration was low already at the beginning of the vernal production. Detectable amounts of phosphate often still occur at that time. The main occurrences of nitrogen-fixing blue-green algae in the open Baltic Sea areas are enhanced by this excess of phosphorus. In June - July the primary production is low and seems to be regulated by the availability of inorganic nitrogen, i.e. ammonium mobilized by decomposition processes or deposited from the atmosphere. Nutrient enrichment experiments with natural Baltic Sea phytoplanktons (Tarkiainen et al. 1974, Tamminen 1982) have shown the deficiency and regulating role of inorganic nitrogen.

Owing to the stable weather conditions in July - August the thermocline is sharp and the upward transport of nutrients by the movement of water from

underneath the thermocline is restricted. If upwelling and/or strong mixing do not disturb this harmony, primary production decreases to a low level. Remineralized phosphorus and nitrogen are soon assimilated by phytoplankton, and are thus often non-detectable. At this stage blue-green algae become dominant. The results described in Chapter 2 and 3 represent the above situation.

The anoxic bottom water layers which frequently occur in the deep basins of the Baltic Sea cause denitrification and, as such, a loss of nitrogen from the nutrient store at the same time as phosphorus is stored in the anoxic layers. After being transported to the surface these water masses contain a low N:P ratio which differs from that assimilated by primary producers (Tarkiainen et al. 1974).

However, observations of artificial changes in the N:P ratio, e.g. from areas with an input of phosphorus like the Uusikaupunki area (Rinne et al. 1981), have shown that bodies of water with a low N:P ratio and an excess of phosphorus mainly contain nitrogen- fixing, blue-green algae. In this case the nitrogen and phosphorus concentrations were high enough for reliable analytical results. Another indirect observation can be found in the northern part of the Gulf of Bothnia, where the inorganic N:P ratio is high and the phosphorus concentration low. Blue-green algal blooms do not occur in that area (Niemi 1979, Rinne et al. 1981).

Composition, species and distribution of the blooms. The species composition of a blue-green algal bloom and the vertical and areal distribution of the species seem to be quite similar from one year to another. This appears to be true, not only during years with heavy blooms, but also in years when the abundance of algae is quite low (Rinne et al. 1979). Furthermore, *Nodularia* occurs generally in the open sea area, while *Aphanizomenon* occurs abundantly also in coastal areas. For hydrographical reasons, heavy blooms mainly consisting of *Nodularia* have been carried by wind and currents from the open sea areas to coastal areas and washed up on the shores (e.g. in 1984). The material is not originally produced in the coastal areas. This phenomenon was clearly seen in August 1984. The heavy mass occurrence of *Nodularia* already observed during our cruise turned to a bloom in the Gulf of Finland, and the weak SE winds transported the blooms towards the Finnish coast. Floating sludge of decaying *Nodularia* was reported from swimming beaches in Porvoo, Helsinki and Hanko.

High abundances of *Aphanizomenon* have even been found in the cold season (already Levander 1900). Heterocysts in these trichomes are few in number, at least in spring (Mikaela Forsskåhl, 1987, Tvärminne Zoological Station, personal communication). Blooms of *Nodularia* have been observed only in July - August. The trichomes of *Nodularia* always contain heterocysts. *Nodularia* seems to be more dependent on higher water temperatures than *Aphanizomenon*. During the cruises a mass occurrence of *Aphanizomenon* was found in the lower part of the euphotic layer, and even at 50 metres close to the permanent halocline (Rinne et al. 1979, 1981; also observed by Woloszynka 1935). However, this species may cause heavy blooms in autumn in the Gulf

of Finland, as e.g. in autumn 1969 after the strong upwelling of deep water rich in phosphorus (e.g. Kaiser & Schulz 1975, Niemi 1975).

All these observations point at a different ecology and the lack of competition between these algae. The two dominant algae, *Aphanizomenon* and *Nodularia*, could be expected to compete especially for phosphorus. However, these algae often occur at different depths (Fig. 9). A somewhat simplified picture of the vertical distribution of the mass occurrences in the transect is presented in Fig. 10. N*odularia* usually caused the blooms in summer, and *Aphanizomenon* occurred simultaneously at greater depths.

In situ and *in vitro* measurements. Although the present results are from July - August, *in vitro* measurements of nitrogen fixation in the open Baltic Sea were performed throughout the growth period in 1985 (Rinne et al. in prep.). According to our comparisons between *in situ* and *in vitro* results, *in vitro* measurements can be used instead of *in situ* measurements for calculating nitrogen fixation in the surface water during the daytime. In our earlier reports a factor of 1.05 was used to convert *in vitro* results into *in situ* results. In this factor only results from the Helsinki archipelago were used. However, the conversion factors from the surface layer 0.88, 1.3 and 1.0 for 1980, 1982 and 1984 respectively, are acceptable.

Rate of nitrogen fixation. The amount of nitrogen fixed by blue-green algae has been evaluated earlier (Rinne et al. 1978). According to the present results, the amounts of nitrogen fixed in the warm period of the year (3 months) can be roughly estimated as follows:

Gulf of Finland	5000 tons
northern Baltic Proper	20000 "
central Baltic Proper	40000 "
southern Baltic Proper	40000 "

These figures concur very well with our previous estimations (Rinne et al. 1978):

Gulf of Finland	10000 tons
northern Baltic Proper	40000 "
central Baltic Proper	30000 "

Only open sea observations were used in making these rough estimations. Although data are available from the coastal areas, ecological models developed from coastal waters (e.g. Plinski 1981) cannot be applied directly to the open Baltic Sea.

Differences between years. Our results from 1974 through several study years and cruises show marked fluctuations between the study years (Table 6). It is difficult to identify trends on the basis of our material concerning both

nitrogen fixation and the abundance or composition of blue-green algae. Neither does the material collected by Lindahl et al. (1978, 1980) reveal any significant year-to-year trends. The values given by Lindahl et al. (1978, 1980) also support this opinion.

TABLE 6. Estimation of fixed nitrogen (kg N km^{-2} · 3 $months^{-1}$) (1974, 1975, 1977, 1978 acc. to Rinne et al. (1978); Helsinki archipelago 1974 acc. to Vuorio et al. (1976), 1975 according to Rinne (1976), 1983 and 1984 acc. to Rinne & Korhonen (1985).

Sub-area	1974	1975	1977	1978	1980	1982	1983	1984
Open sea								
Gulf of Finland	-	350	300	43	170	38	-	490
Northern Baltic Proper	400	310	1000	-	700	130	-	2600
Central Baltic Proper	760	19	-	-	380	430	-	780
Southern Baltic Proper	-	-	-	-	-	440	-	-
Åland Sea	-	380	-	-	-	-	-	-
Bothnian Sea	-	-	-	8	-	-	-	-
Bothnian Bay	-	-	-	1	-	-	-	-
Coastal areas								
Helsinki archipelago	170	120	-	-	-	-	190	250

According to the few results we obtained from the southern Baltic Sea in 1982, the nitrogen fixation was almost at the same level as that in the Baltic Proper. However, our results are markedly lower than those presented by Hübel & Hübel (1974, 1976a,b, 1987).

It has been suggested that *Nodularia* is an important factor causing eutrophication of the Baltic Sea (e.g. Öström 1976) by increasing the amount of nitrogen available in the ecological cycle in seawater.

Nodularia has a dominant biomass in the southern Baltic Sea areas, as can be seen in Table 2. A change in the share of the total biomass between *Nodularia* and *Aphanizomenon* in the years 1980-1984 in the northern parts of the Baltic Sea can also be discerned. An increase in the total amount of nitrogen fixed in the northern part of the Baltic Sea (Table 6) would then be consistent with the more effective nitrogen fixation of *Nodularia*. Whether this is a trend connected with eutrophication or a coincidence in the sampling at a different ecological stage of the two species, is still an open question.

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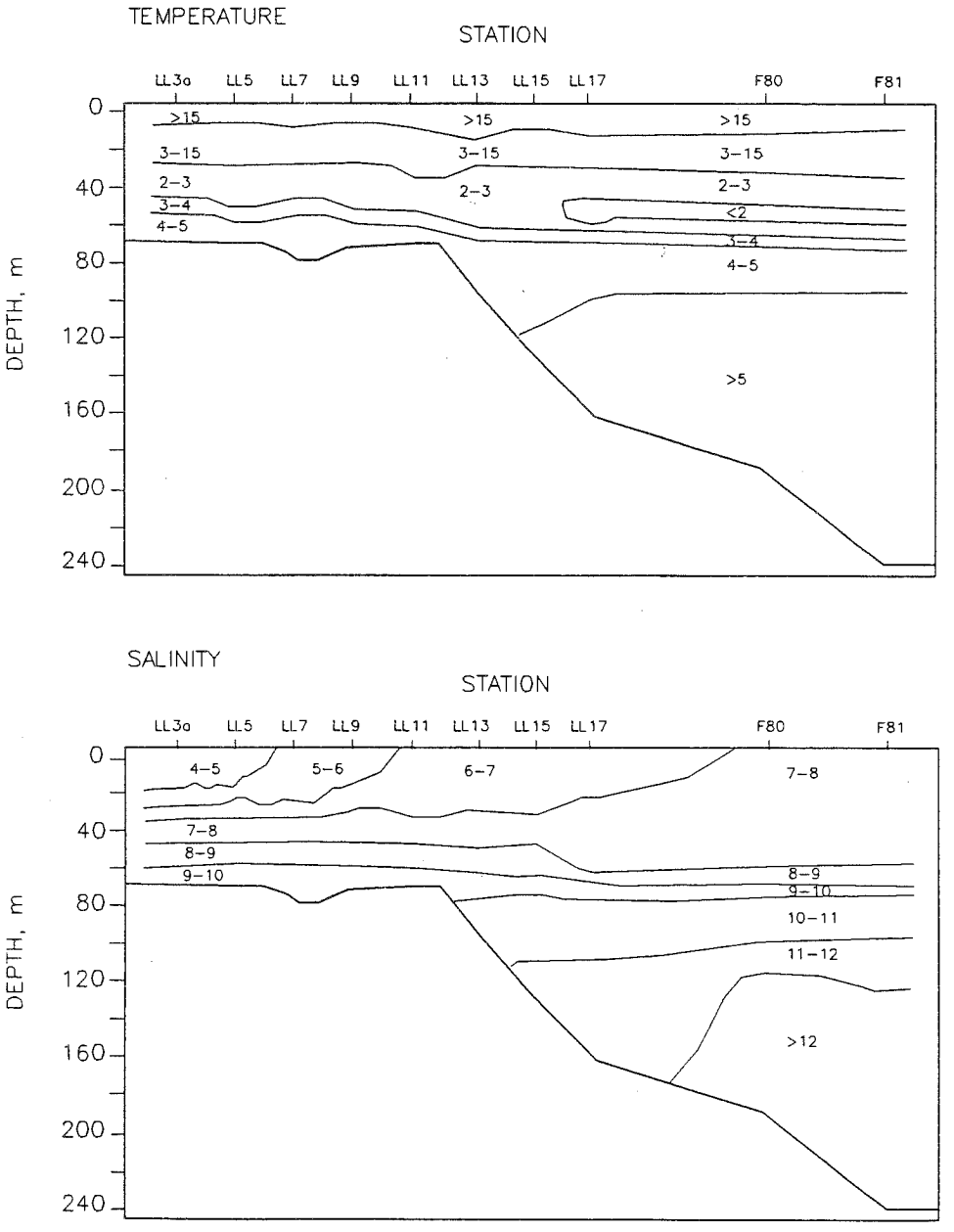


Fig. 2A. Hydrography (T ° C, S °/oo) and nutrients (NH_4-N, NO_3-N, PO_4-P, totP, μmol $\cdot l^{-1}$) at transect LL-3a - F-81, July 27 - July 30, 1980.

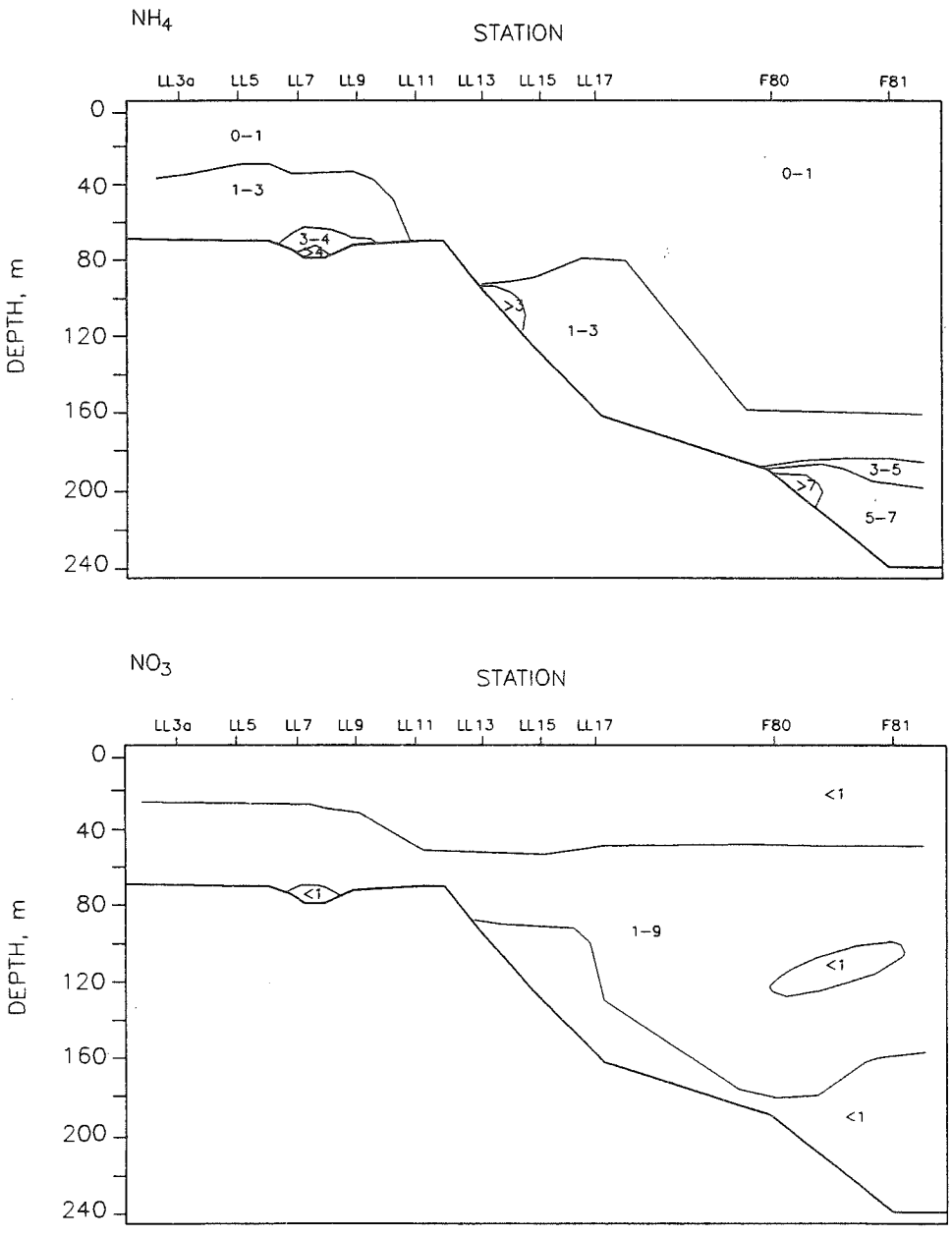


Fig. 2B. Hydrography (T ° C, S °/oo) and nutrients (NH_4-N, NO_3-N, PO_4-P, totP, μmol $\cdot$ l^{-1}) at transect LL-3a - F-81, July 27 - July 30, 1980.

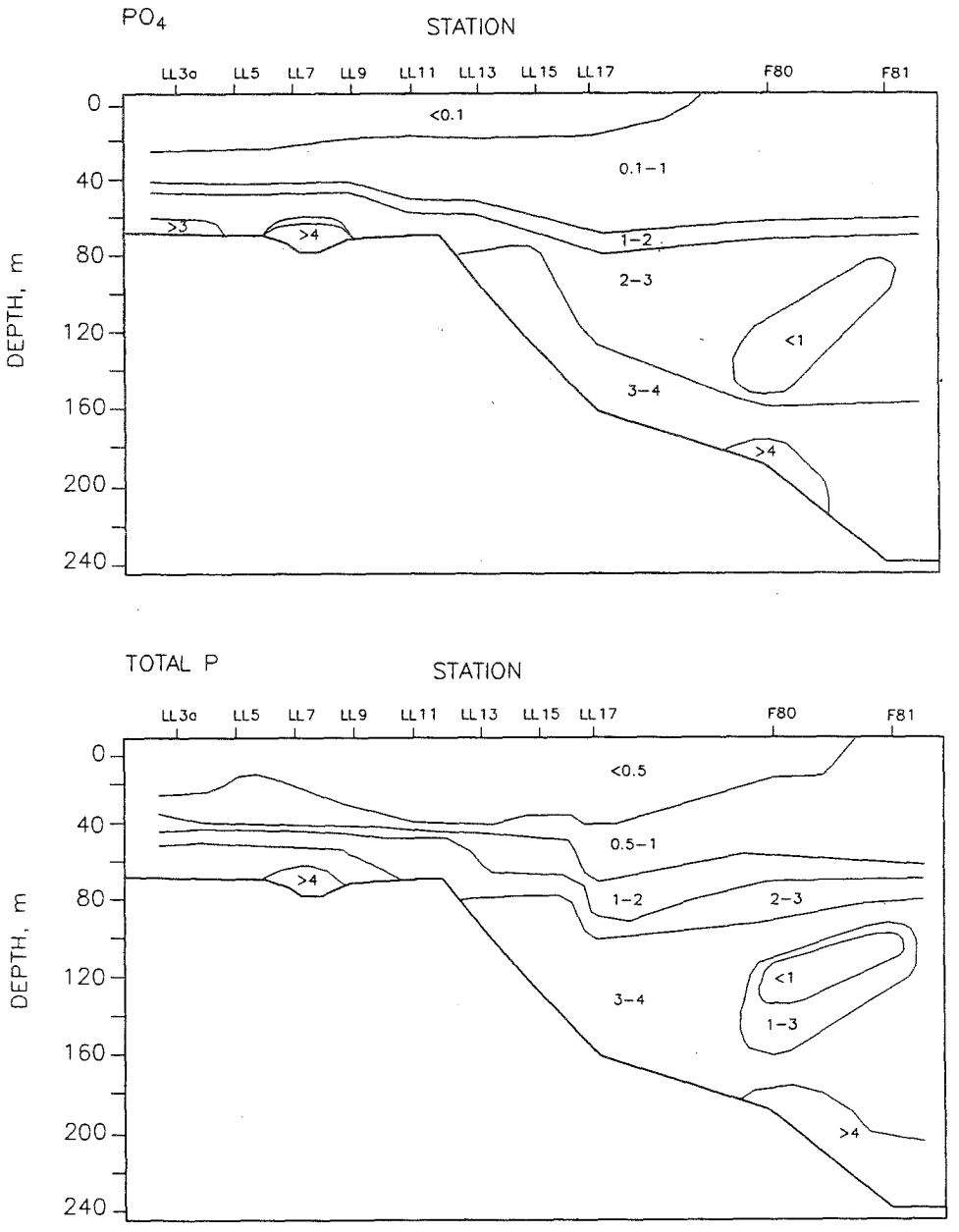


Fig. 2C. Hydrography (T ° C, S °/oo) and nutrients (NH_4-N, NO_3-N, PO_4-P, totP, μmol $\cdot$ l^{-1}) at transect LL-3a - F-81, July 27 - July 30, 1980.

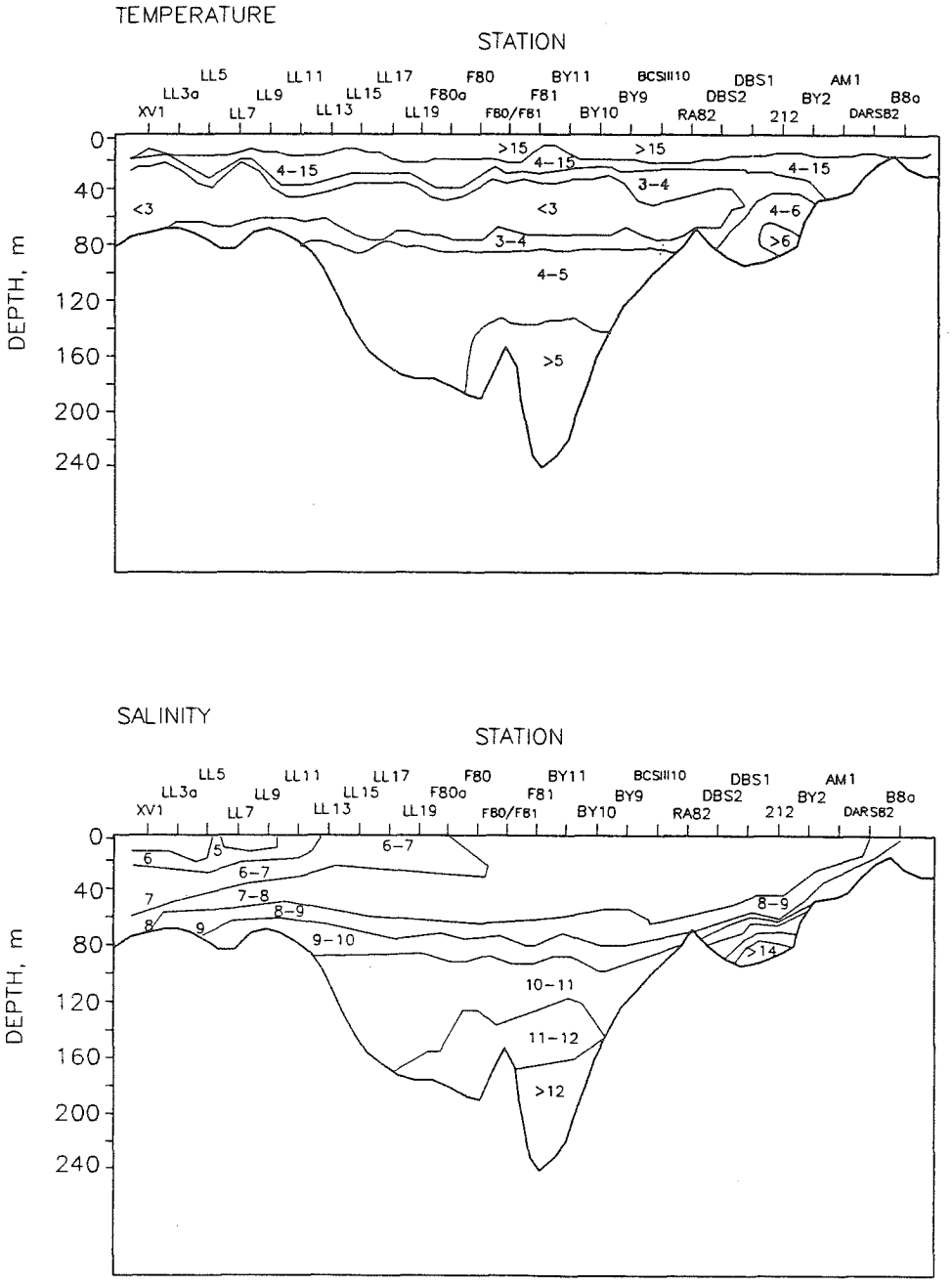


Fig. 3A. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - B-8a, July 27 - August 3, 1982.

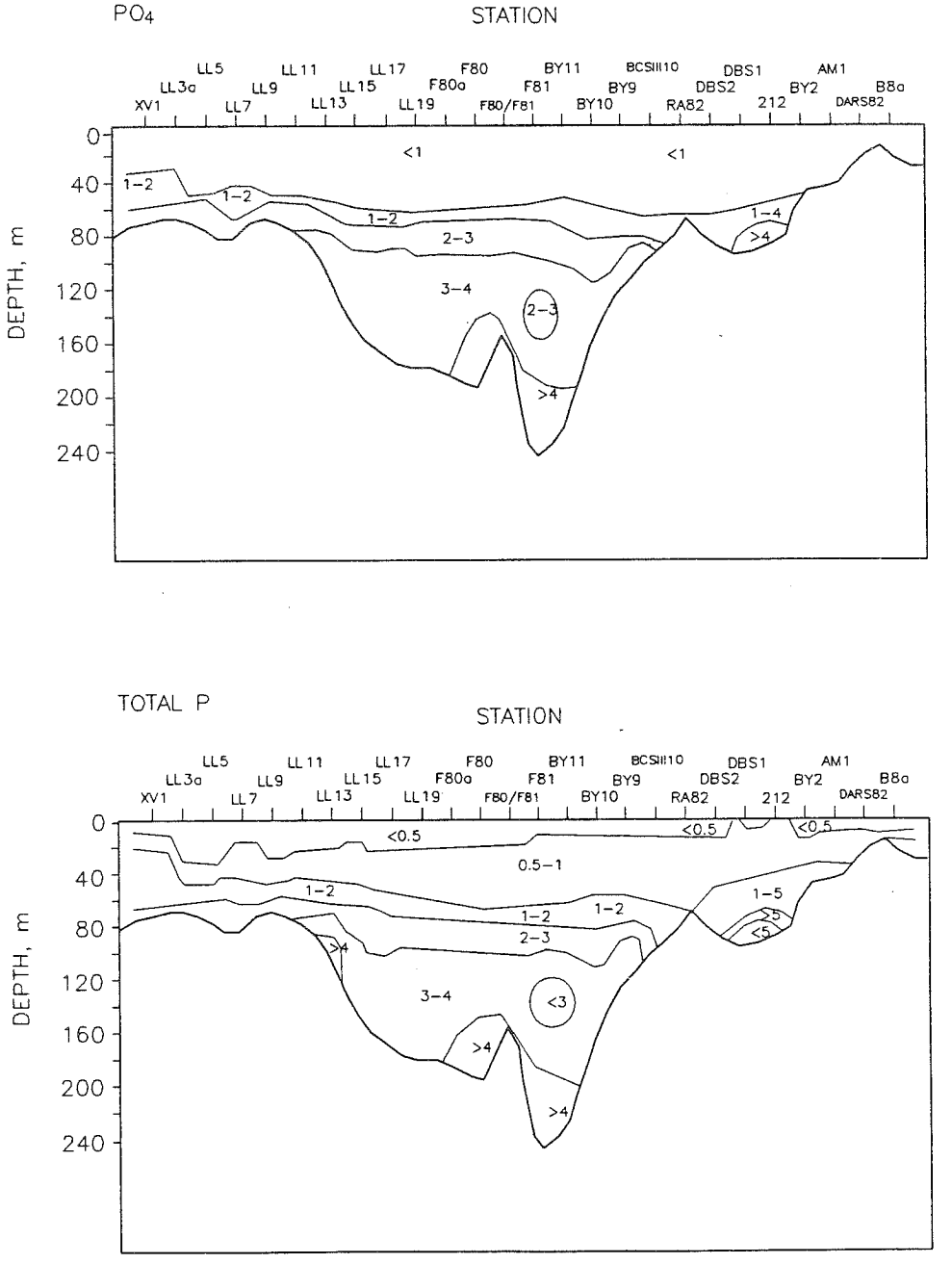
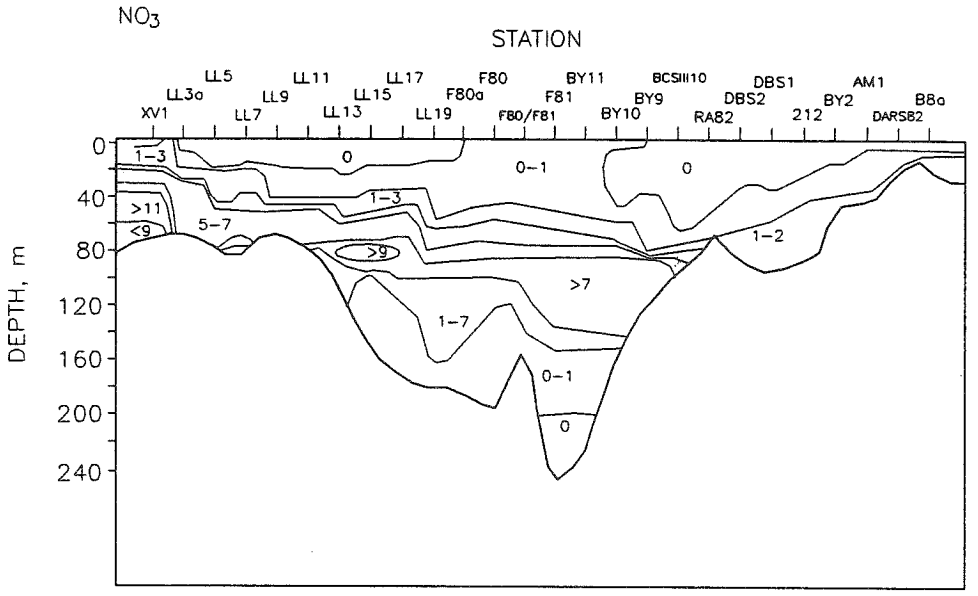


Fig. 3B. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - B-8a, July 27 - August 3, 1982.



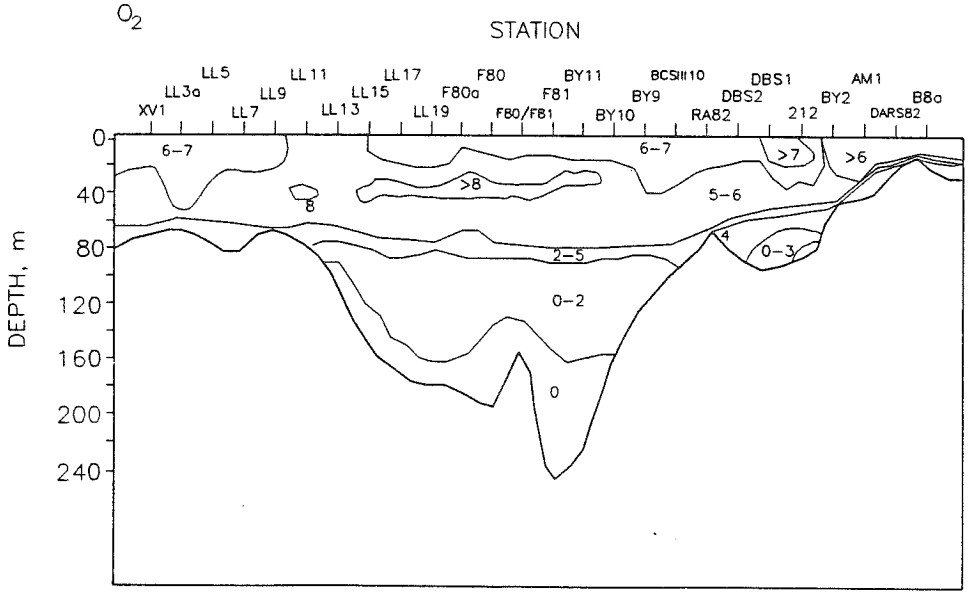


Fig. 3C. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - B-8a, July 27 - August 3, 1982.

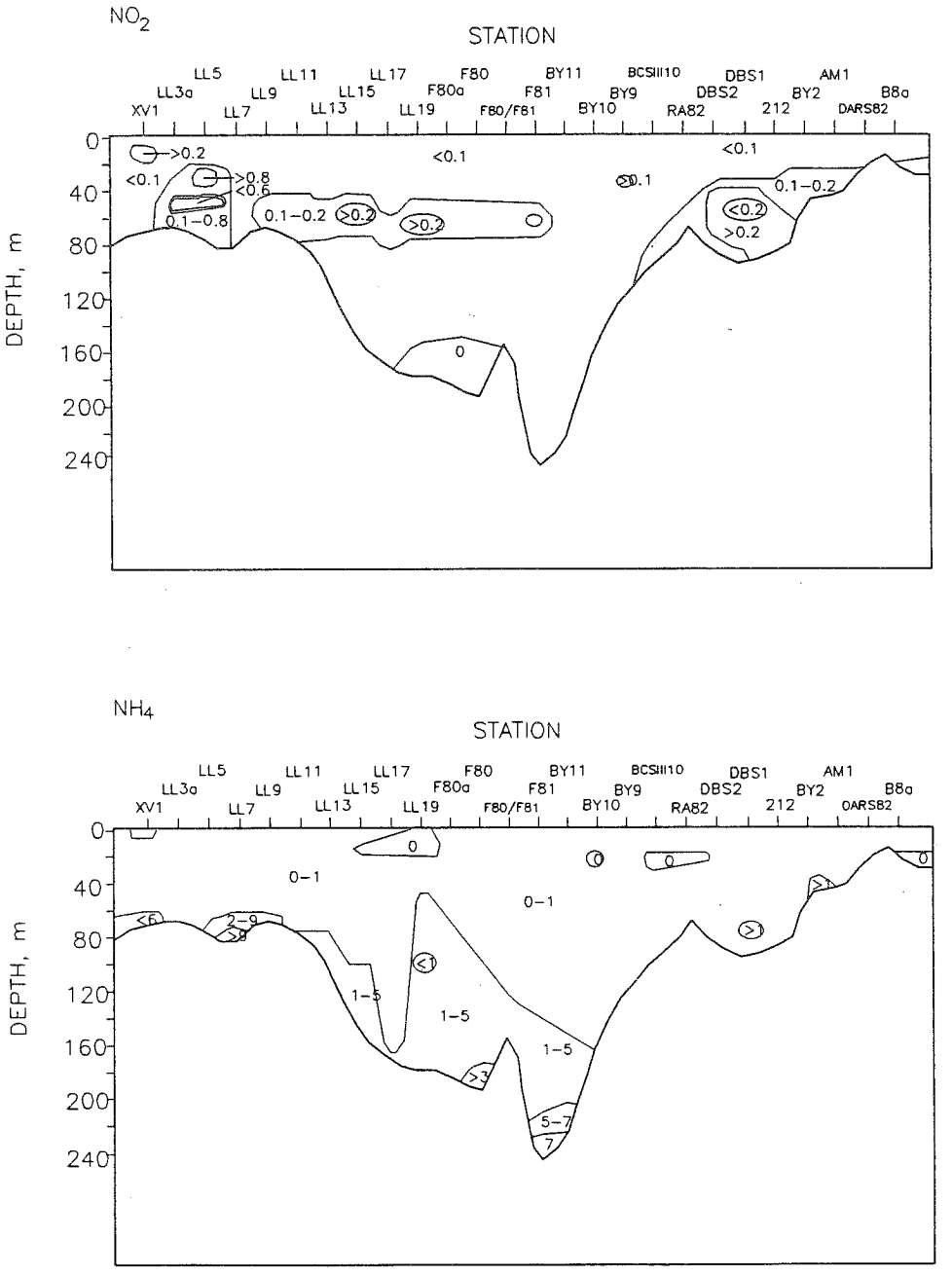


Fig. 3D. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - B-8a, July 27 - August 3, 1982.

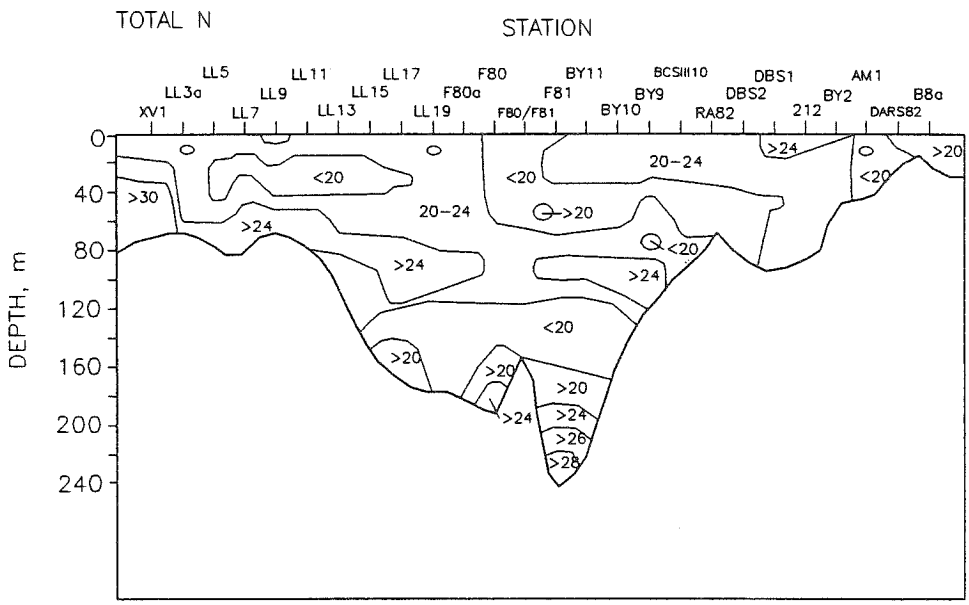


Fig. 3E. Hydrography (T°C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - B-8a, July 27 - August 3, 1982.

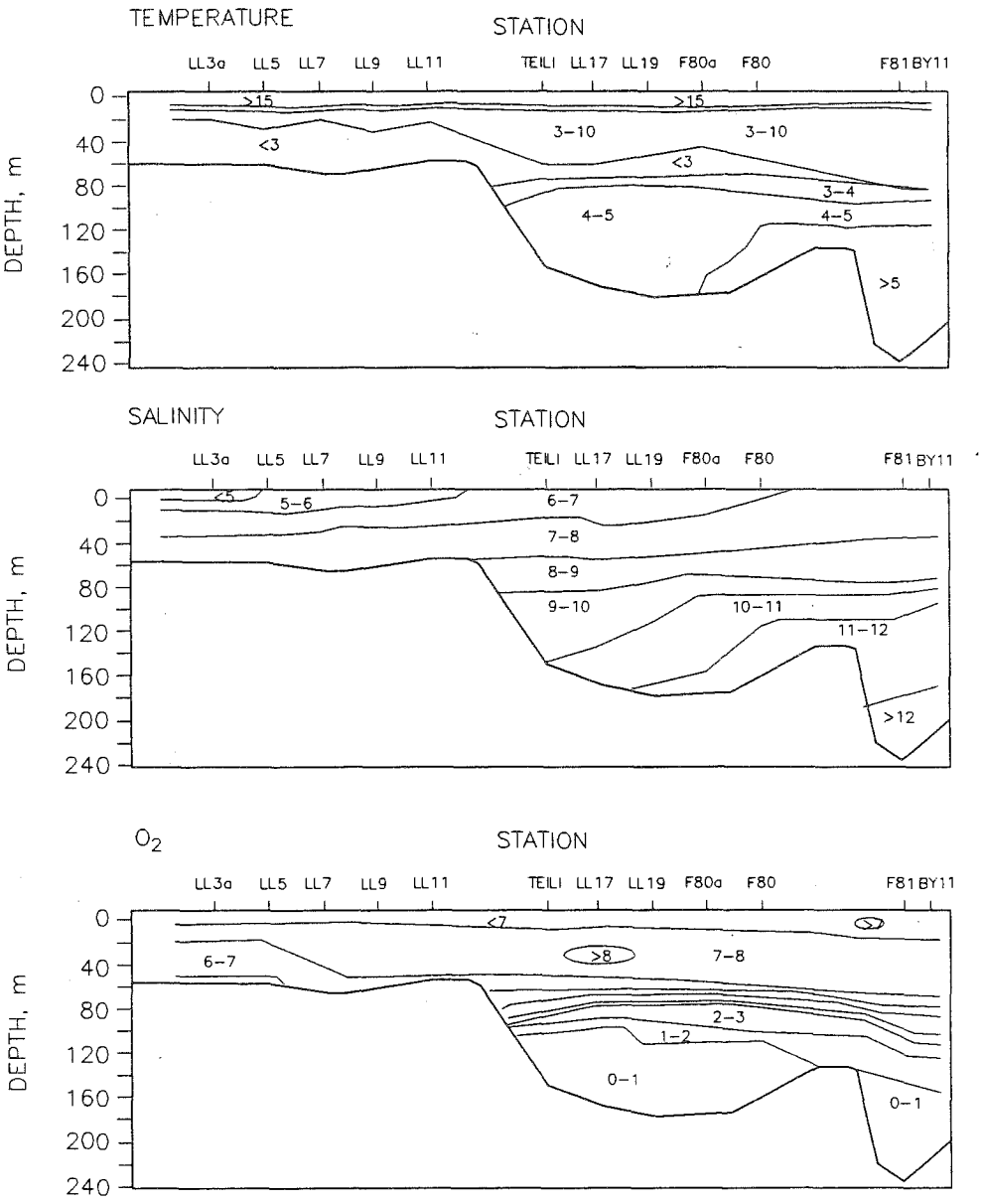


Fig. 4A. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - BY-11, July 24 - 27, 1984.

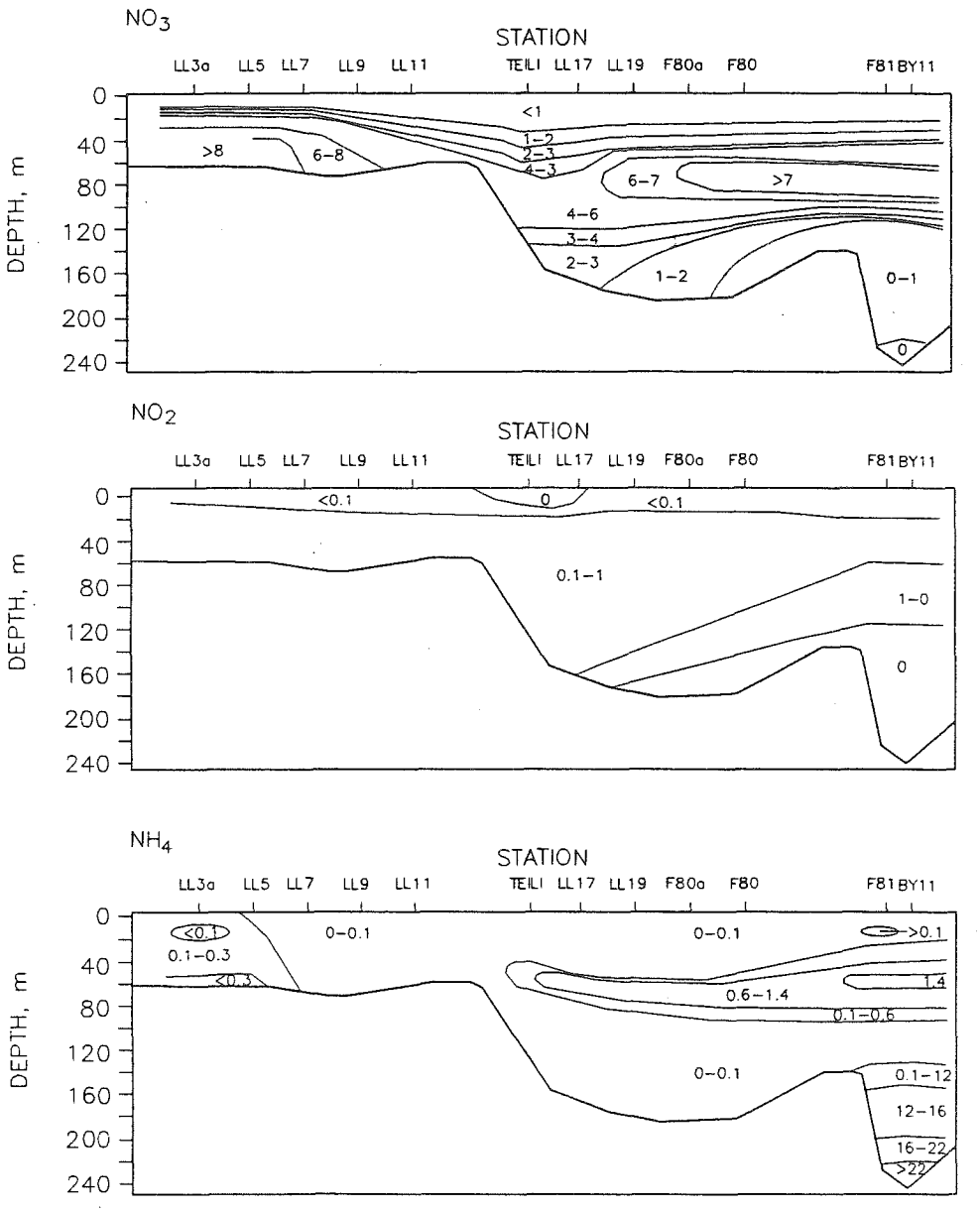


Fig. 4B. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - BY-11, July 24 - 27, 1984.

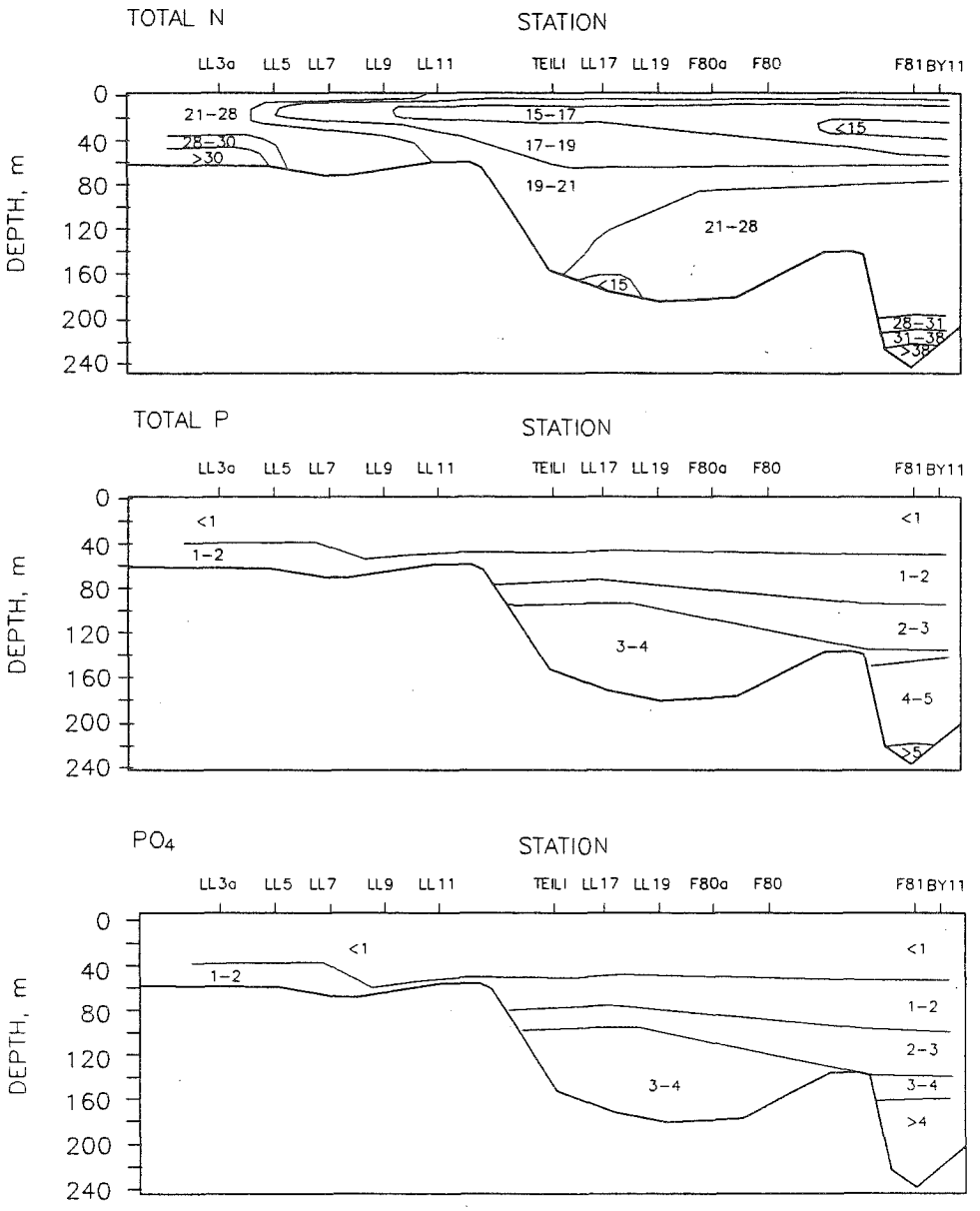


Fig. 4C. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NH_4-N, NO_3-N, NO_2-N, totN, PO_4-P, totP, μmol · l^{-1}) at transect XV-1 - BY-11, July 24 - 27, 1984.

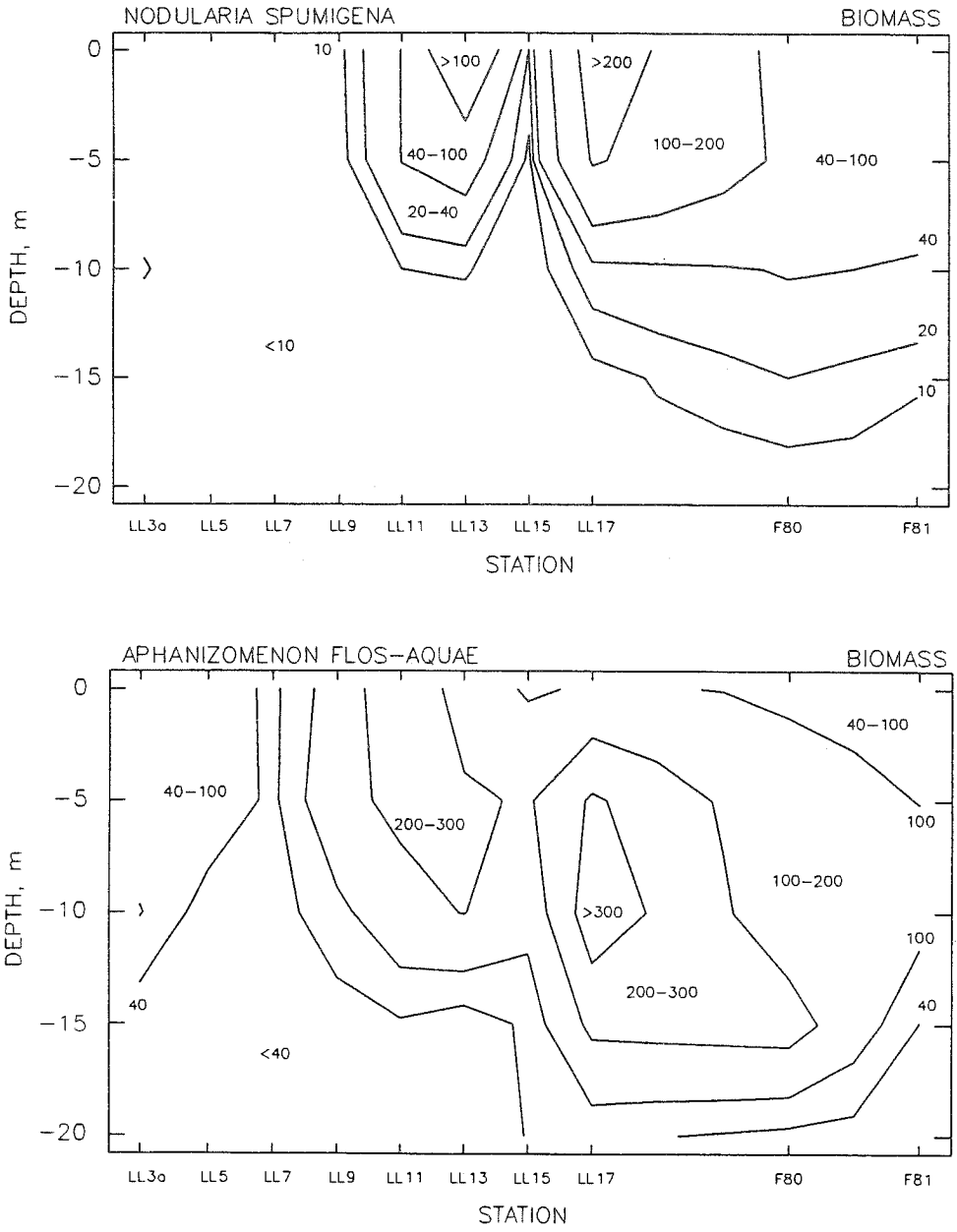


Fig. 5. Biomass (mg · m^{-3}) of Nodularia spumigena and Aphanizomenon flos-aquae along the transect LL-3a - F-81, July 27 - 30, 1980.

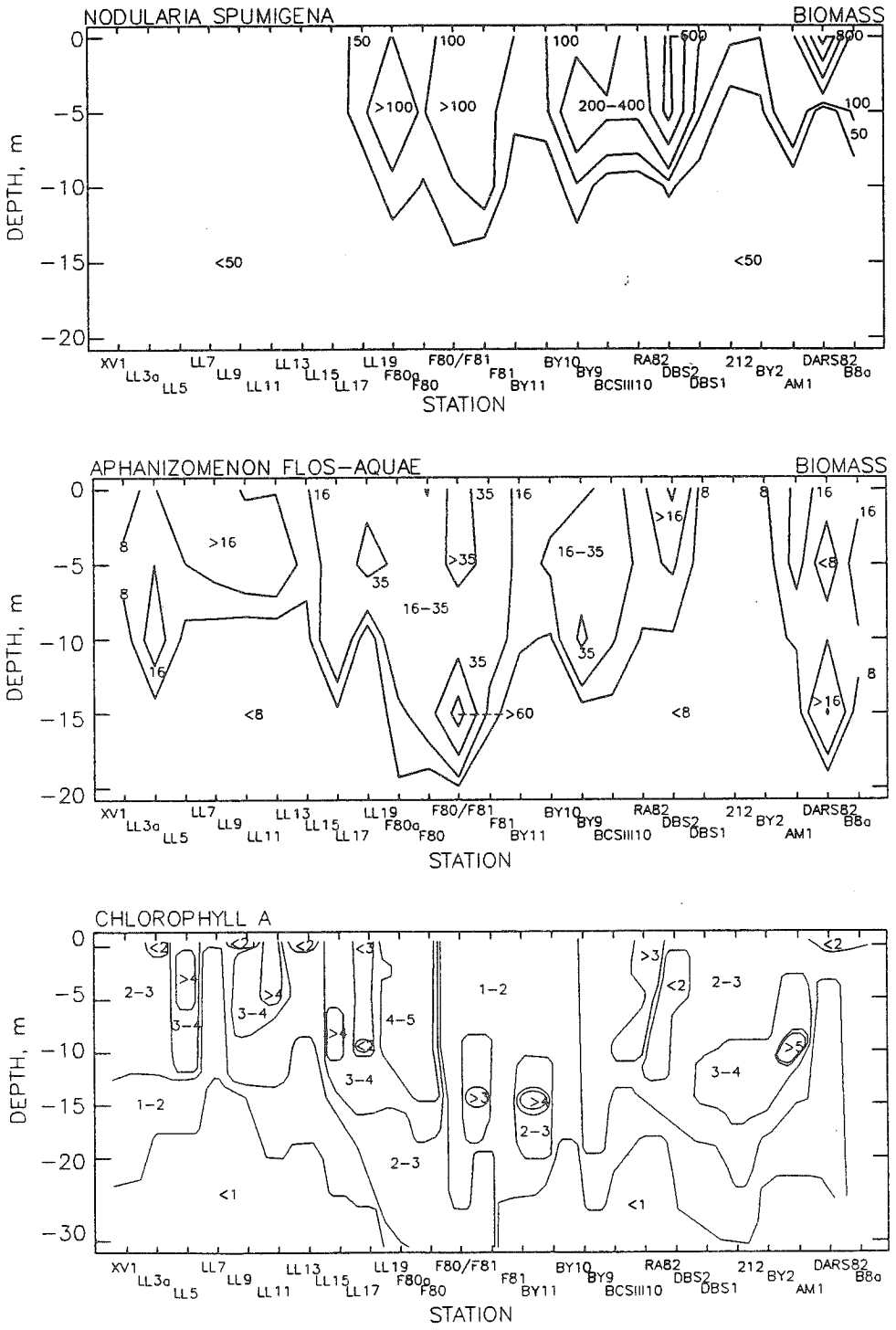


Fig. 6. Biomass (mg · m^{-3}) of Nodularia spumigena and Aphanizomenon flos-aquae and chlorophyll a $\mu g \cdot l^{-1}$ along the transect XV-1 - B-8a, July 27 - August 3, 1982.

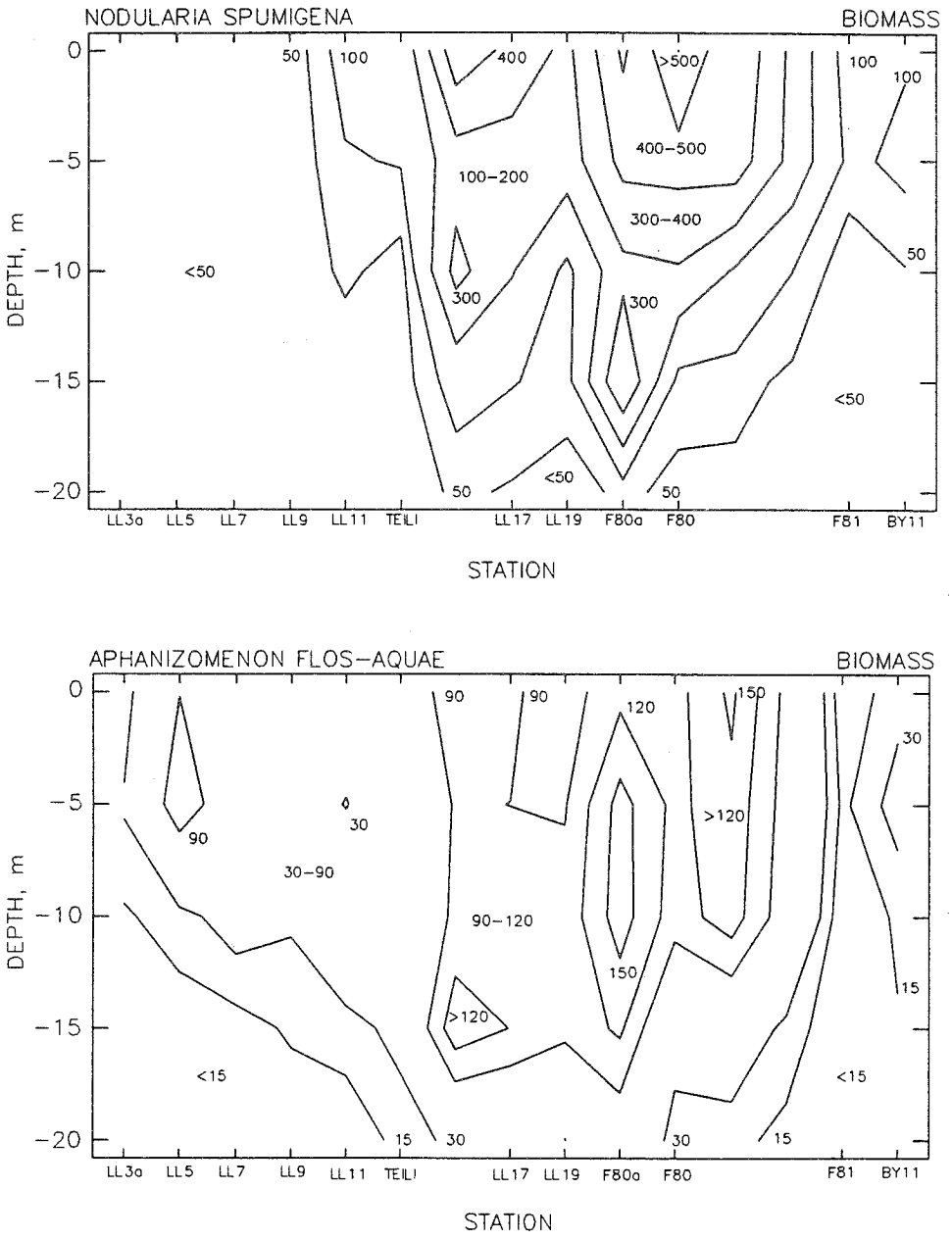


Fig. 7. Biomass (mg · m-3) of Nodularia spumigena and Aphanizomenon flos-aquae along the transect XV-1 - BY-11, July 24 - 27, 1984.

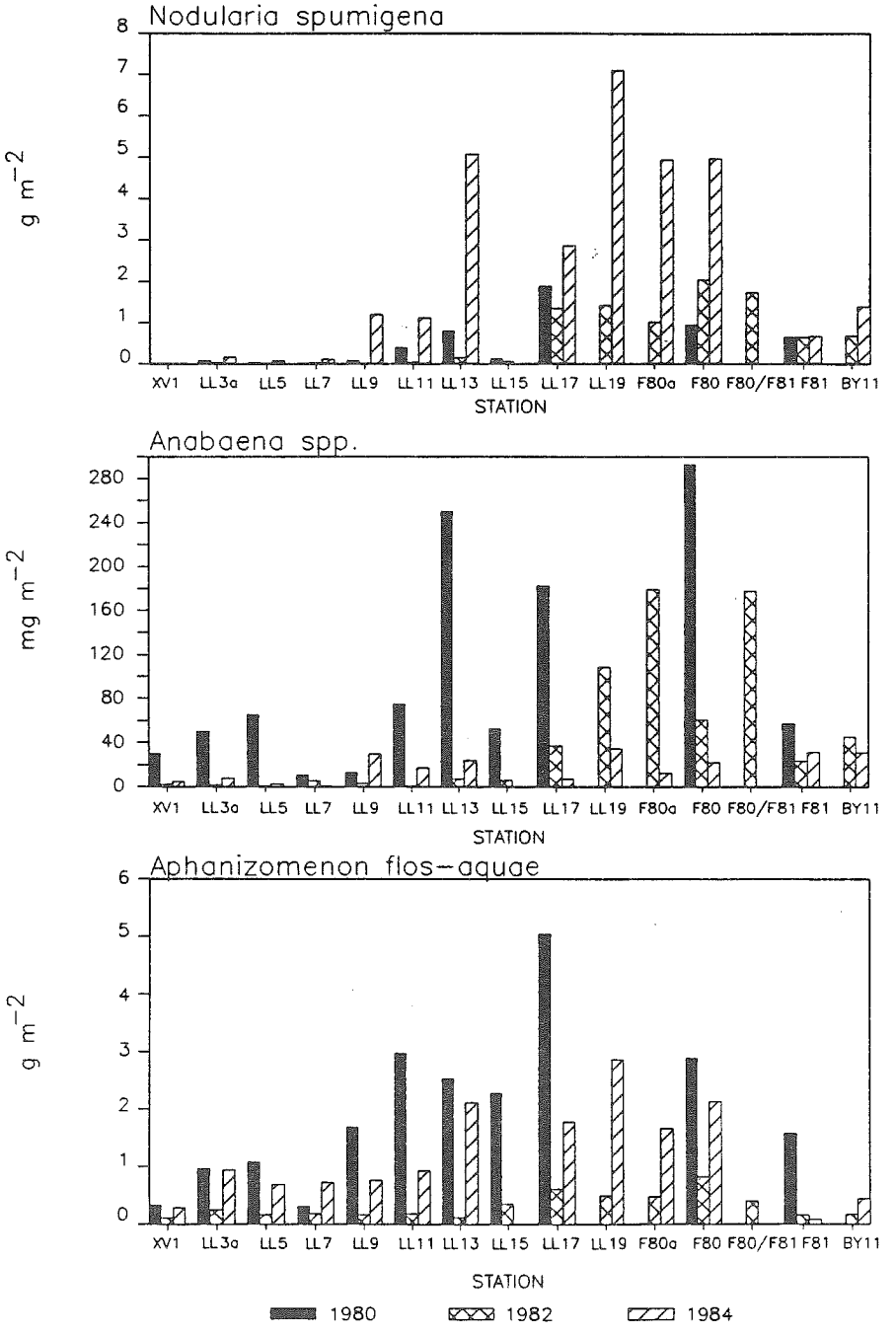


Fig. 8. Distribution of Nodularia spumigena, Aphanizomenon flos-aquae and Anabaena spp. (biomass mg $\cdot$ m^{-2}, 0 - 20 m) along the transects in 1980, 1982 and 1984. In the central and northern Baltic Proper and in the Gulf of Finland Anabaena was chiefly represented by the species A. lemmermannii P. Richter. In the southern and southwestern Baltic also other species occurred, A. cylindrica Lemm., A. inaequalis (Kütz.) Bornet & Flahault and others.

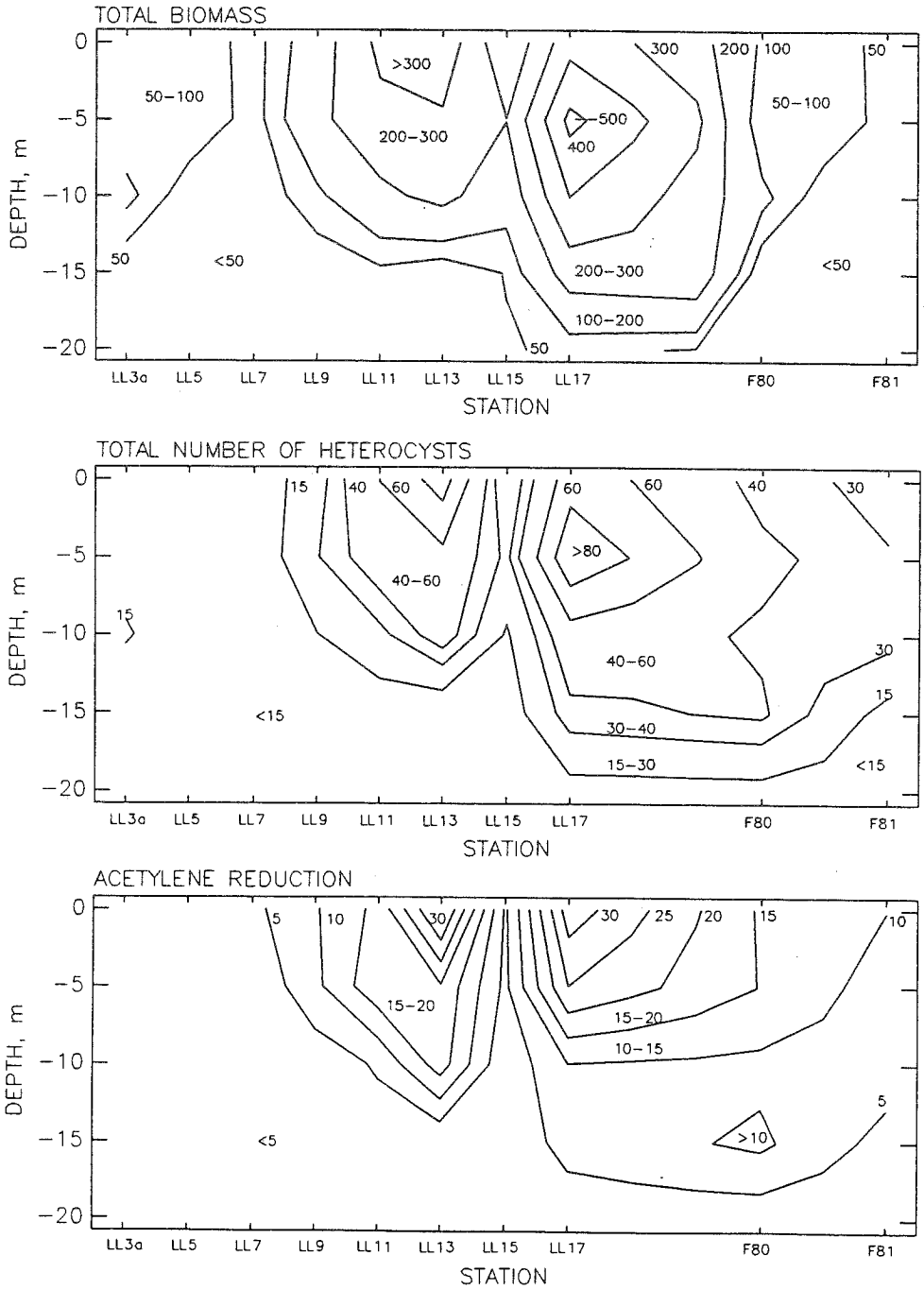


Fig. 11. Total biomass (mg · m^{-3}), total number of heterocysts (10^{-6} · m^{-3}) and acetylene reduction (μmol · $(2\ h)^{-1}$ m^{-3}) along the transect LL-3a - F-81, July 27 - 30, 1980.

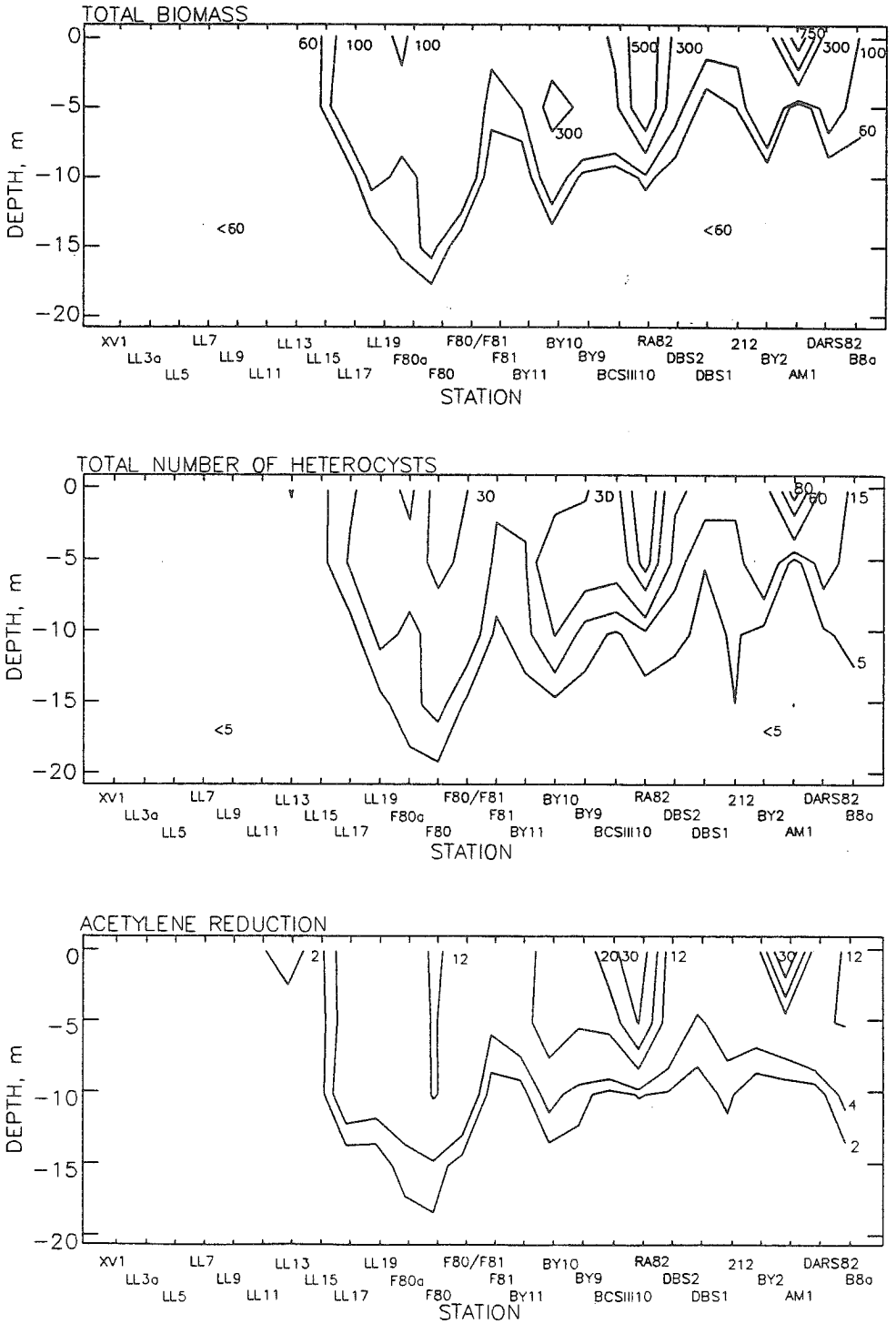


Fig. 12. Total biomass (mg · m^{-3}), total number of heterocysts (10^{-6} · m^{-3}) and acetylene reduction (μmol (2 h)$^{-1}$ m^{-3}) along the transect LL-3a - B 8A, July 27 - August 3, 1982.

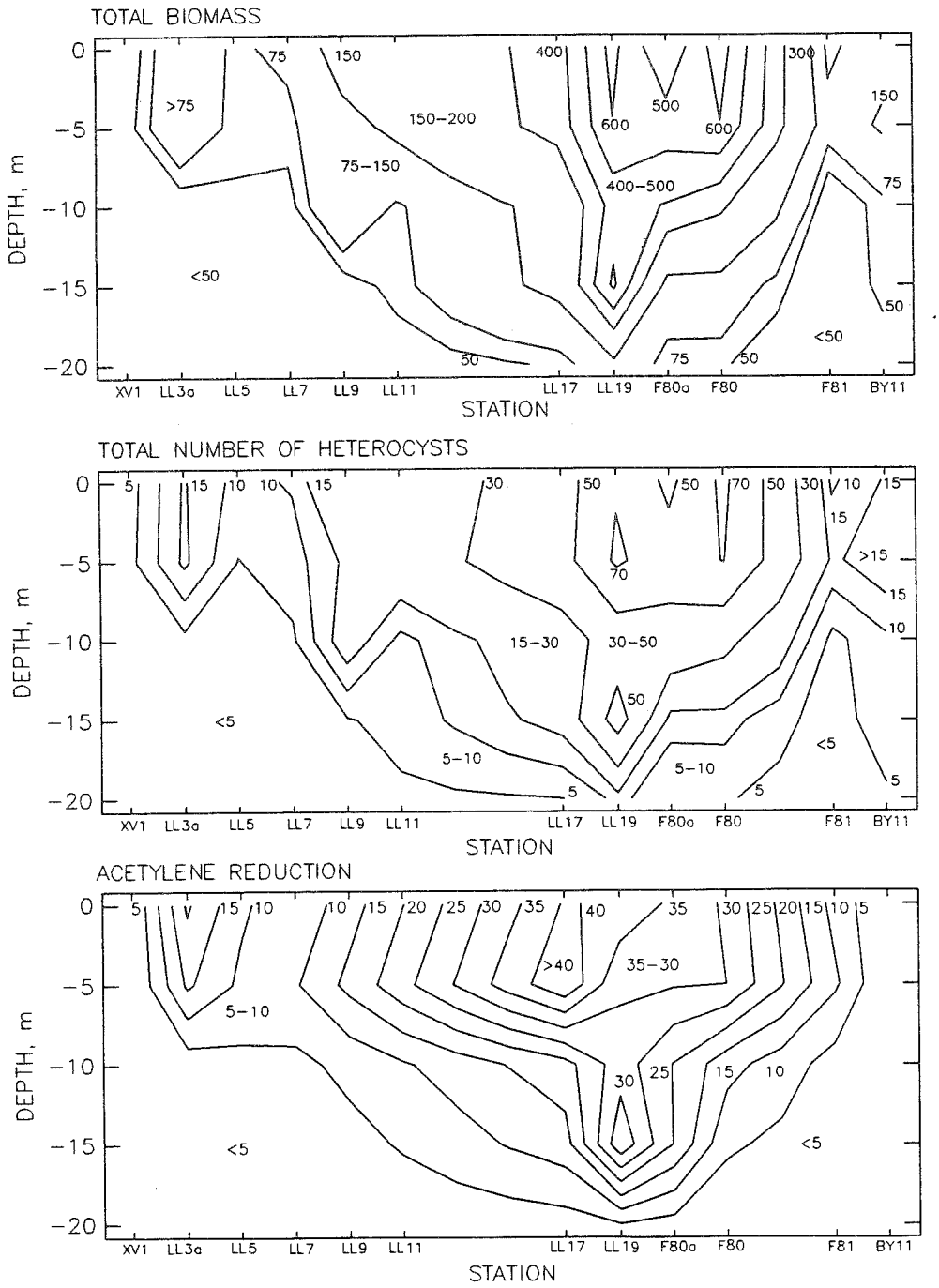


Fig. 13. Total biomass (mg · m^{-3}), total number of heterocysts (10^{-6} · m^{-3}) and acetylene reduction (μmol · $(2\ h)^{-1}$ m^{-3}) along the transect XV-1 - BY-11, July 24 - 27, 1984.

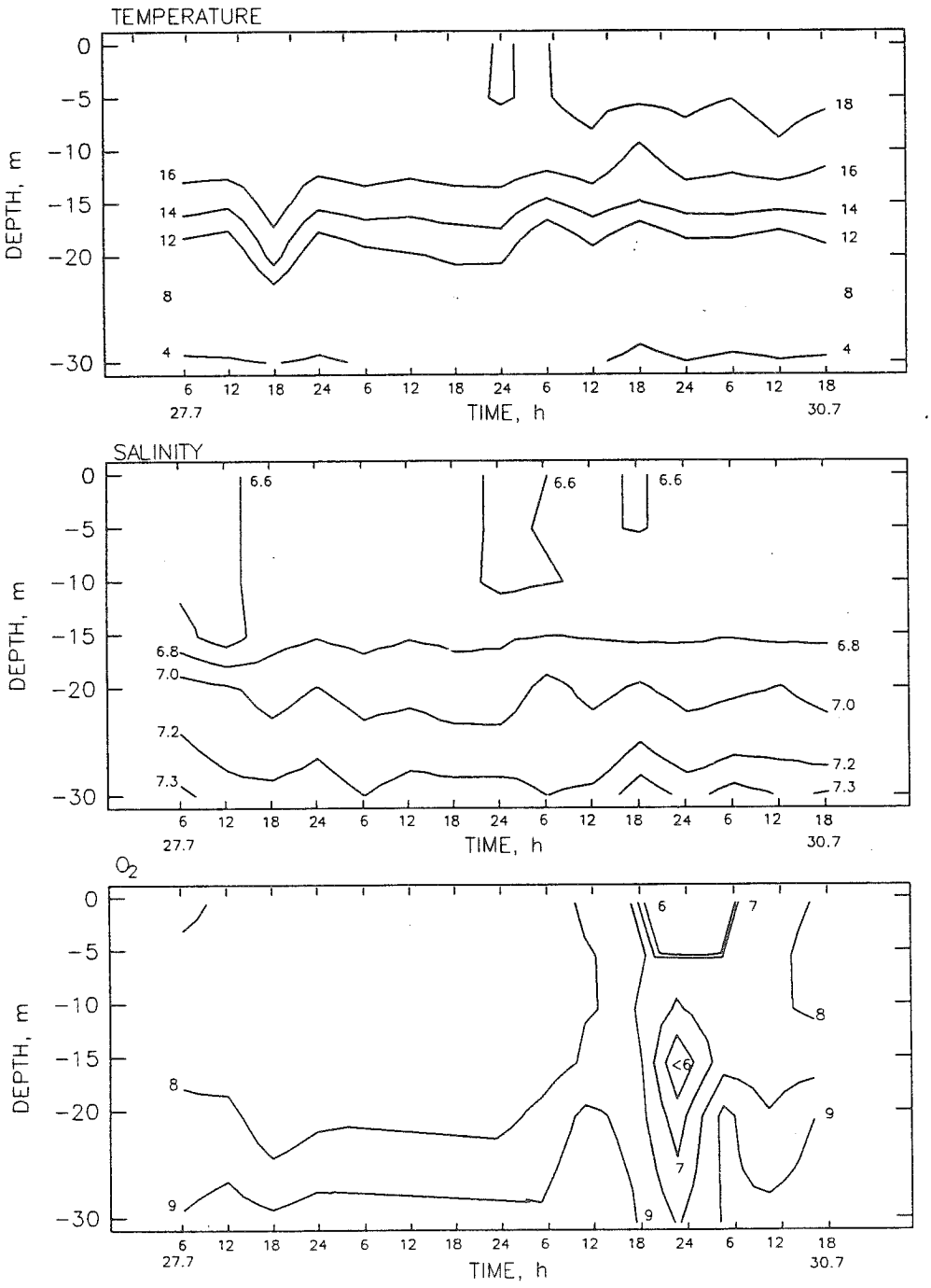


Fig. 14A. Hydrography (T ° C, S °/oo, 0_2 ml · l^{1}) and nutrients (NO_3-N, NH_4-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station ED, July 27 - 30, 1980.

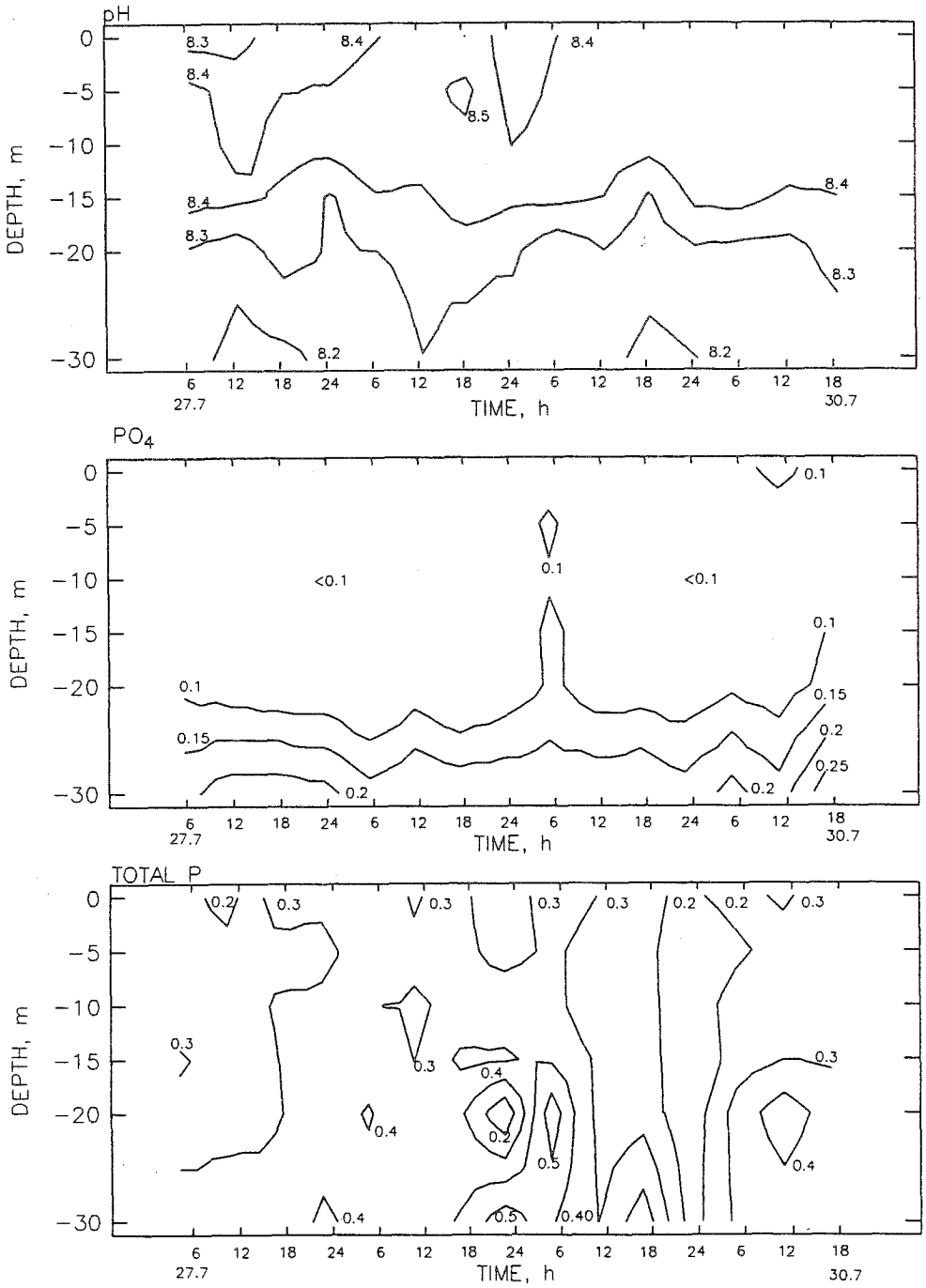


Fig. 14B. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NO_3-N, NH_4-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station ED, July 27 - 30, 1980.

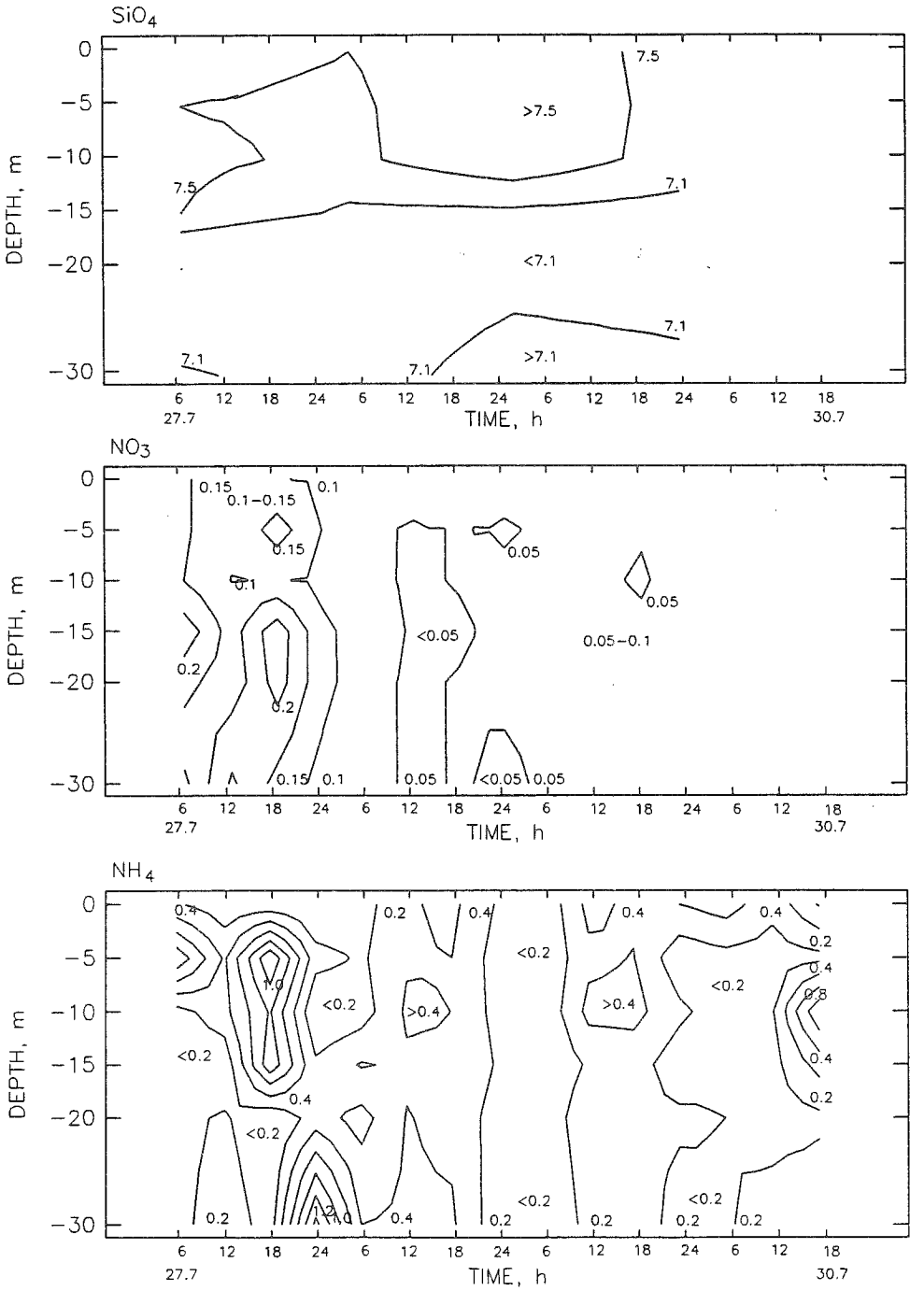


Fig. 14C. Hydrography (T ° C, S °/oo, 0_2 ml · l^{1}) and nutrients (NO_3-N, NH_4-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station ED, July 27 - 30, 1980.

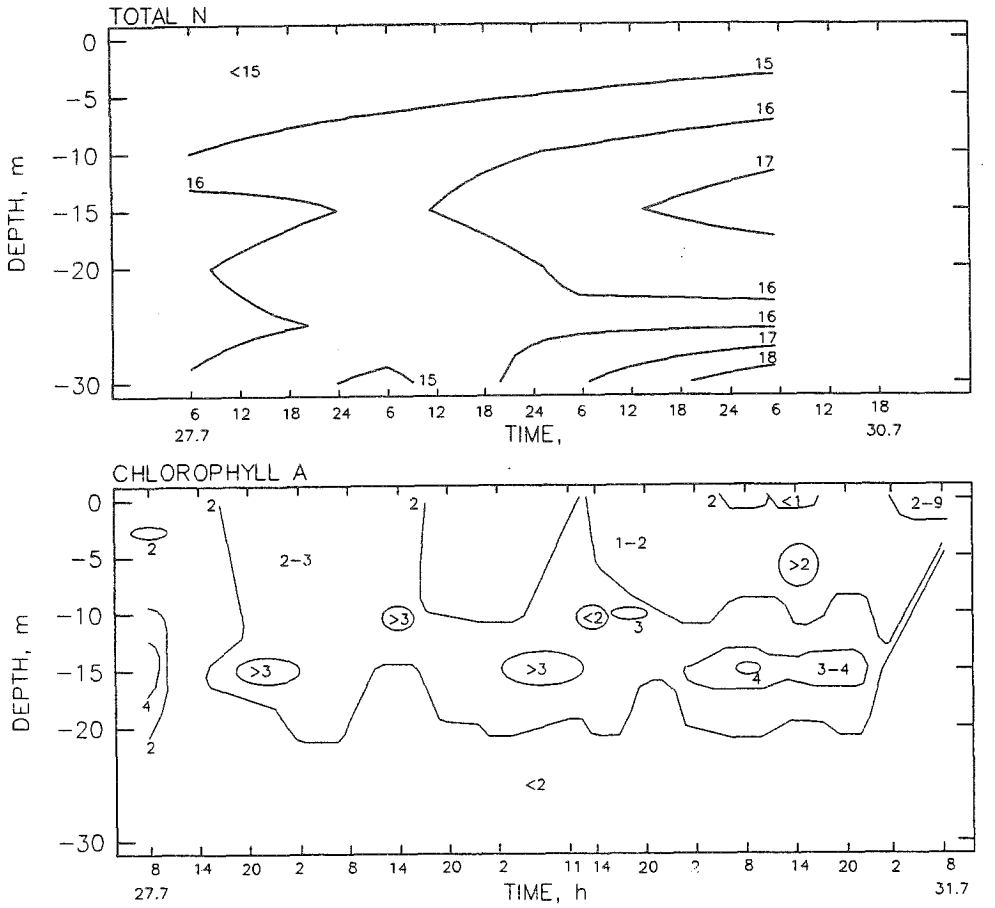


Fig. 14D. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) and nutrients (NO_3-N, NH_4-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station ED, July 27 - 30, 1980.

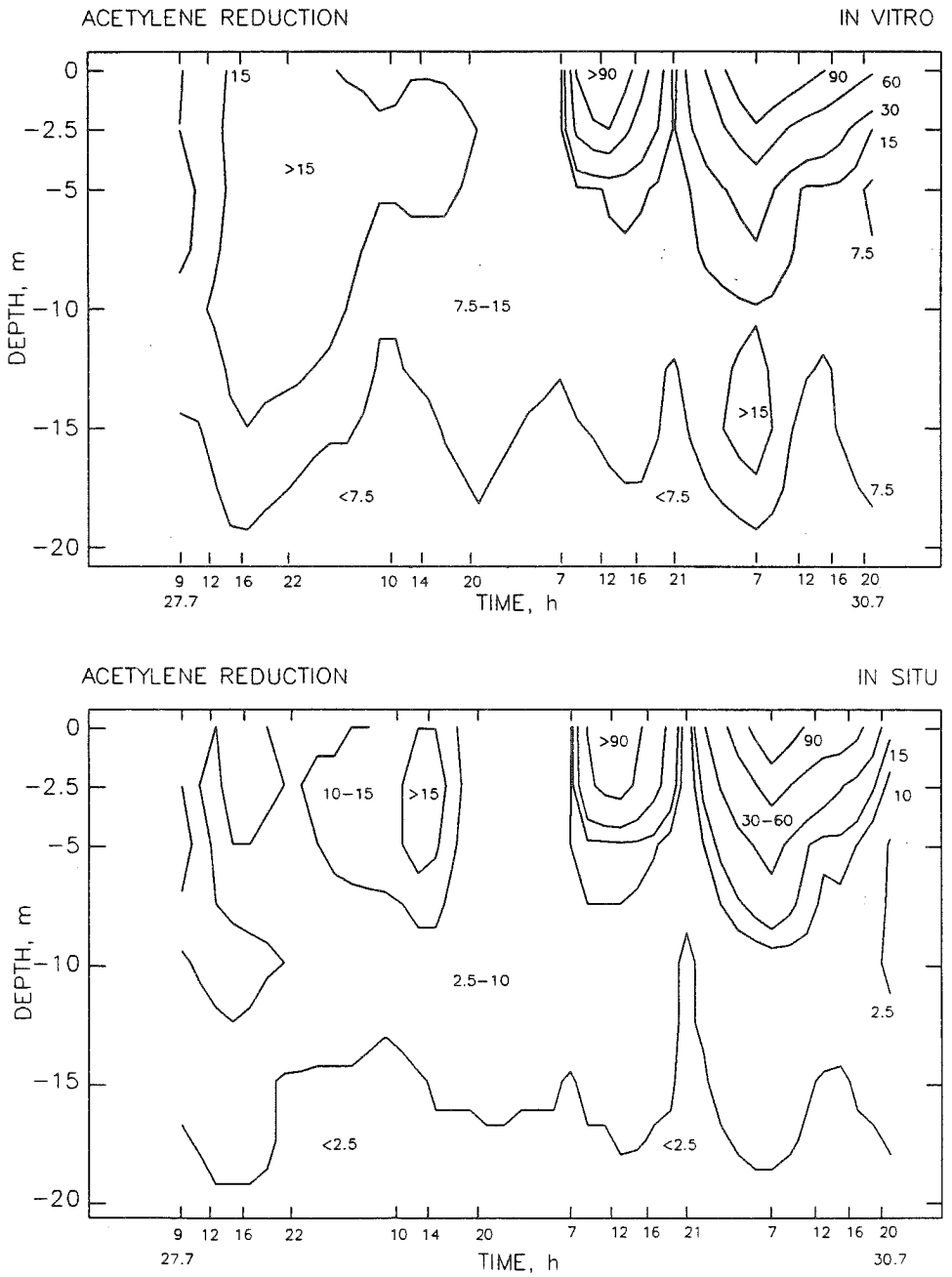


Fig. 15A. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena, Aphanizomenon flos-aquae and Anabaena spp., and acetylene reduction rate in situ and in vitro (μmol · $(2\ h)^{-1}$ m^{-3}) at the anchor station ED, July 27 - 30, 1980.

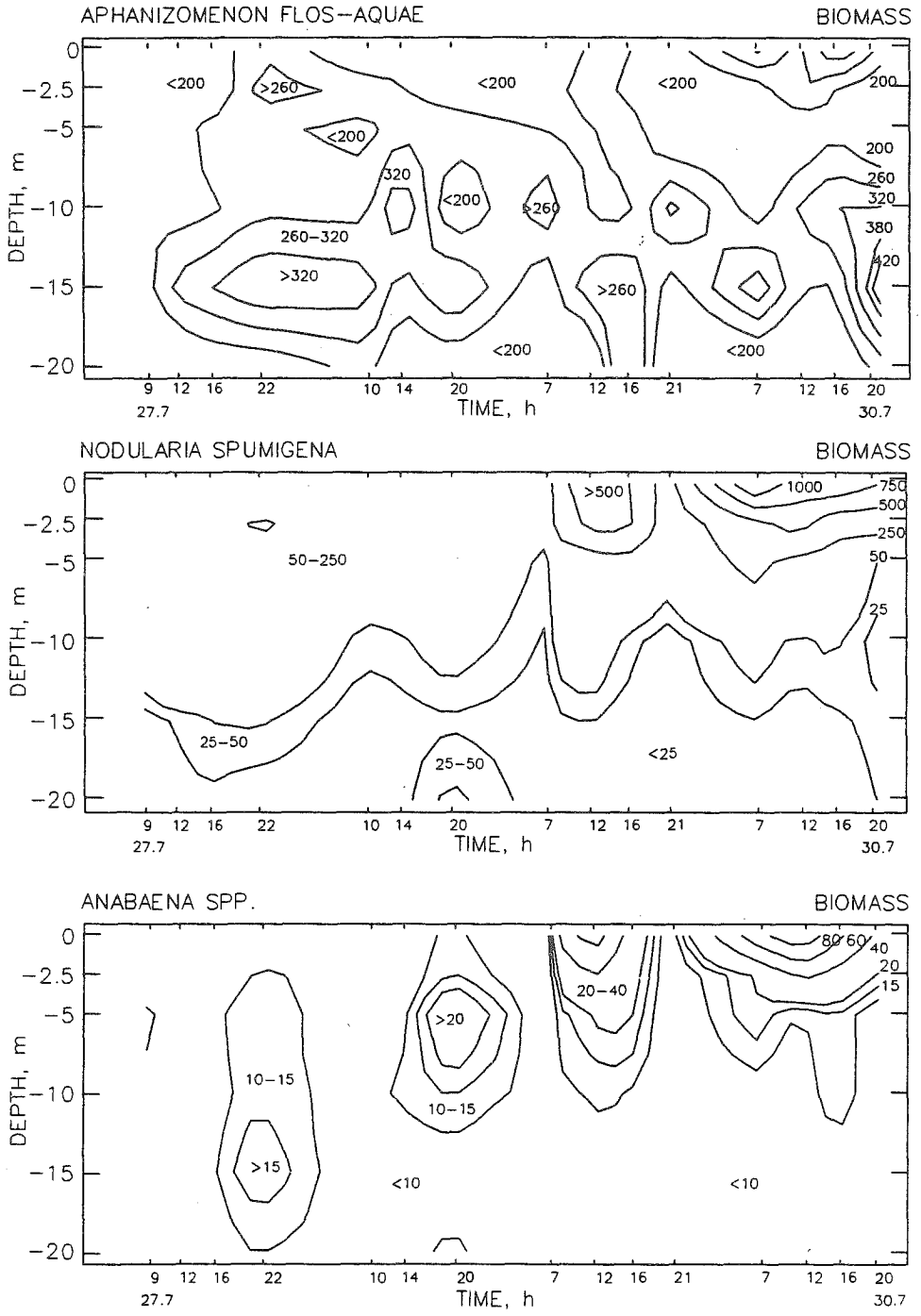


Fig. 15B. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena, Aphanizomenon flos-aquae and Anabaena spp., and acetylene reduction rate in situ and in vitro (μmol · $(2\ h)^{-1}$ m^{-3}) at the anchor station ED, July 27 - 30, 1980.

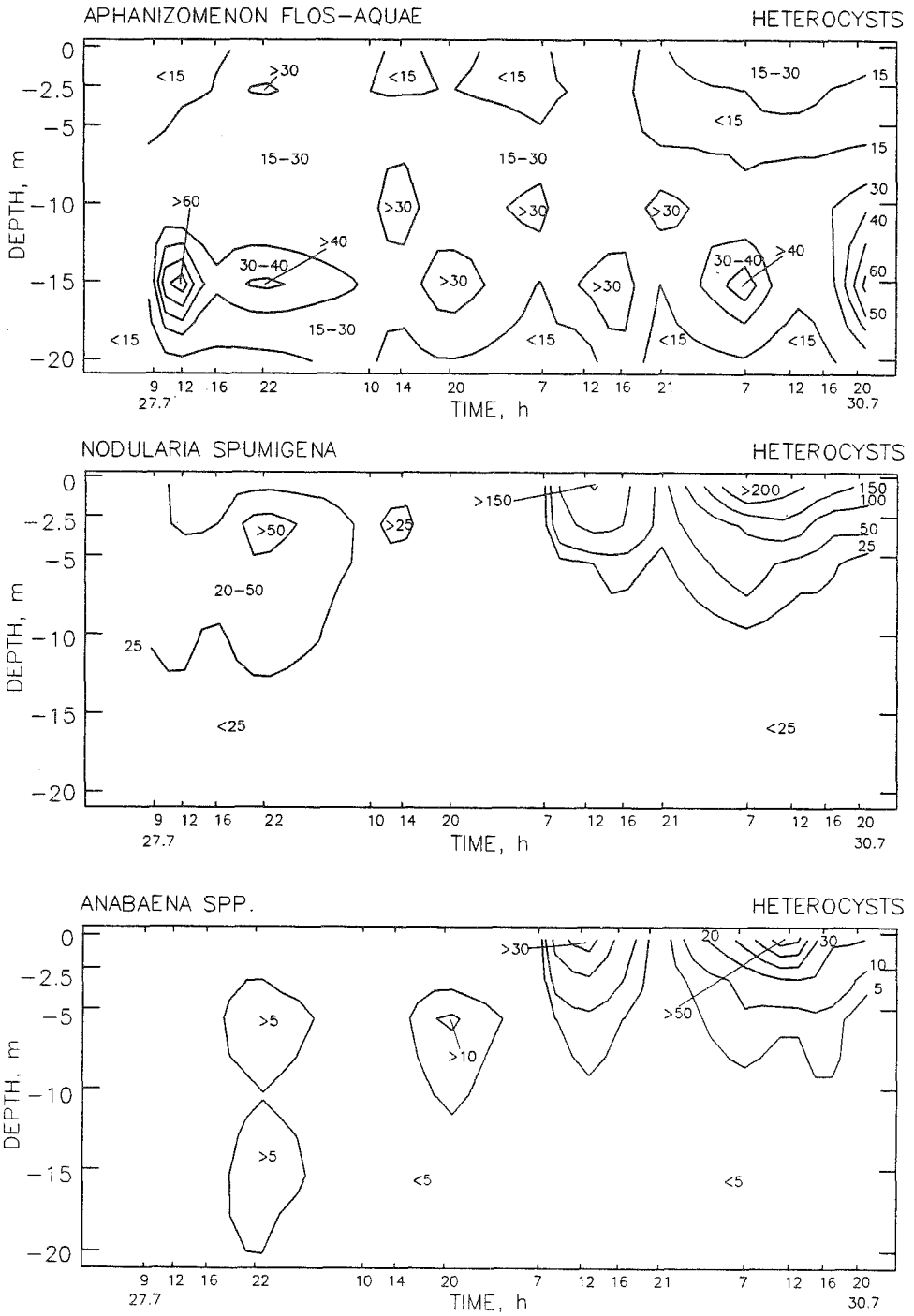


Fig. 15C. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena, Aphanizomenon flos-aquae and Anabaena spp., and acetylene reduction rate in situ and in vitro (μmol · $(2\ h)^{-1}$ m^{-3}) at the anchor station ED, July 27 - 30, 1980.

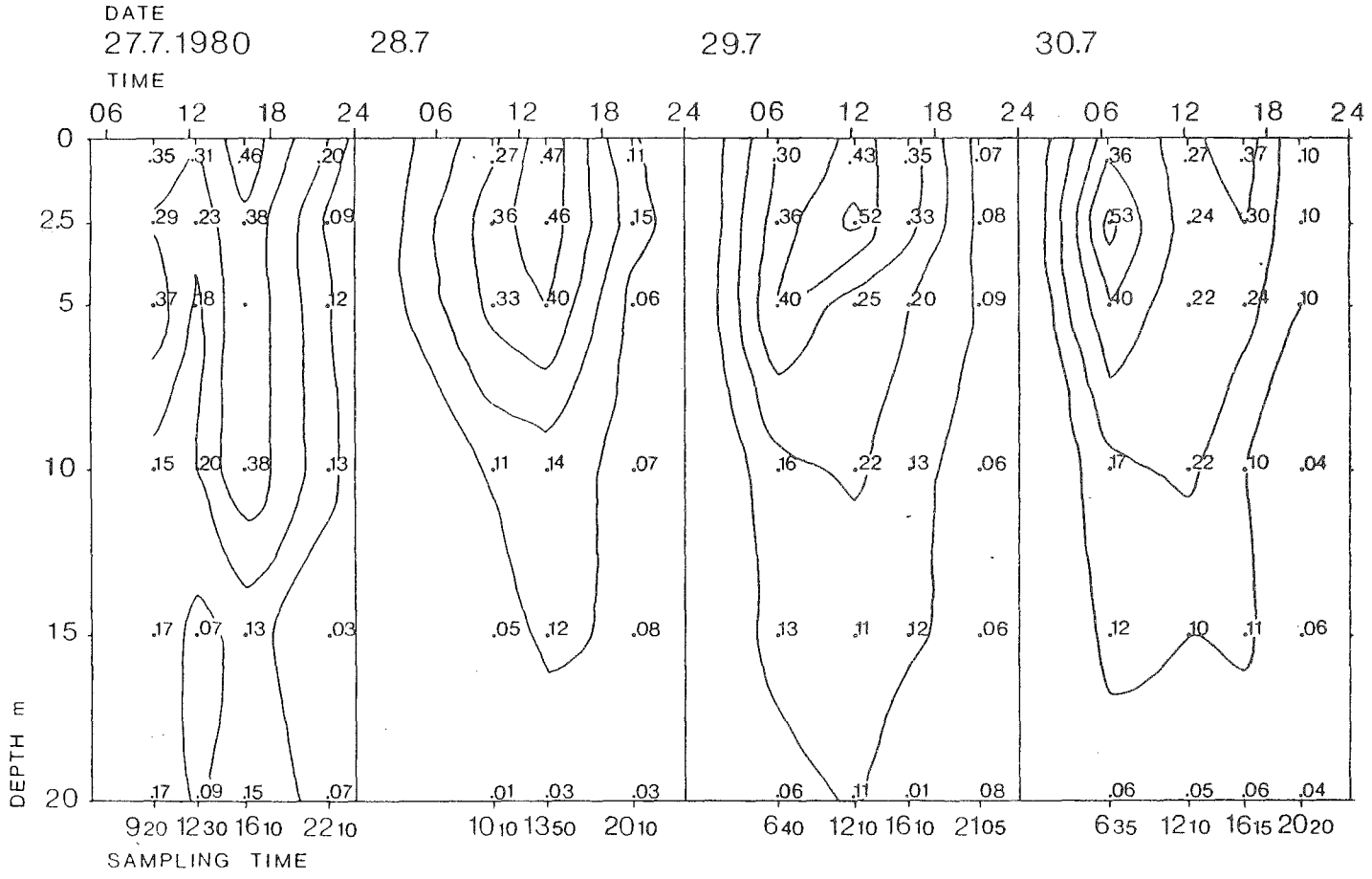


Fig. 16. Heterocystic activity of heterocysts of blue-green algae (pM C_2H_2 (red.) (2h het.)$^{-1}$) in samples from 0, 2.5, 5, 10, 15 and 20 m at the anchor station ED in 1980 (July 27 - 30). (Adopted from Rinne & al. 1984.)

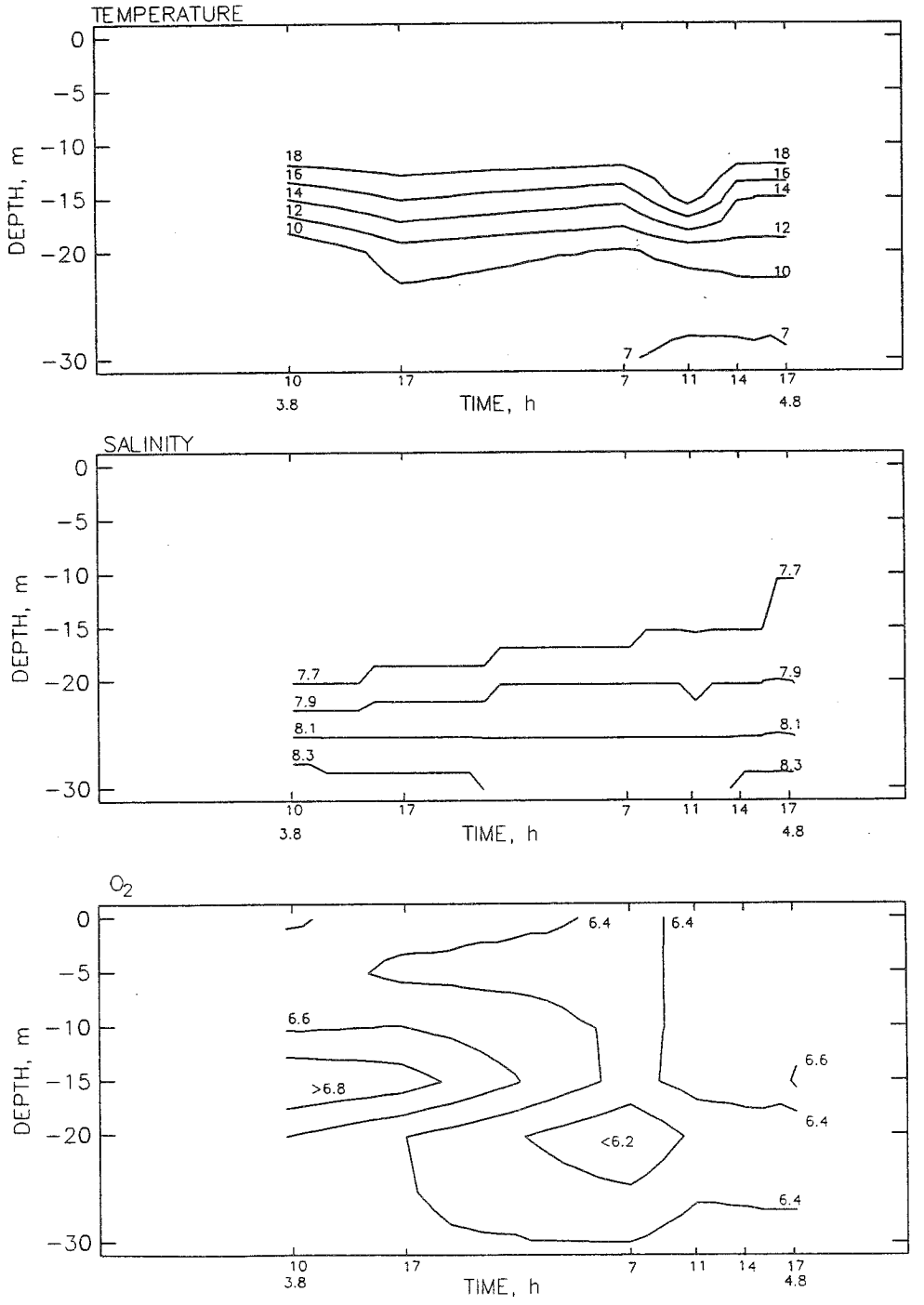


Fig. 17A. Hydrography (T ° C, S °/oo, 0_2 ml · l^{-1}) pH and nutrients (NH_4-N, NO_2-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station Caliatta, August 3 - 4, 1982.

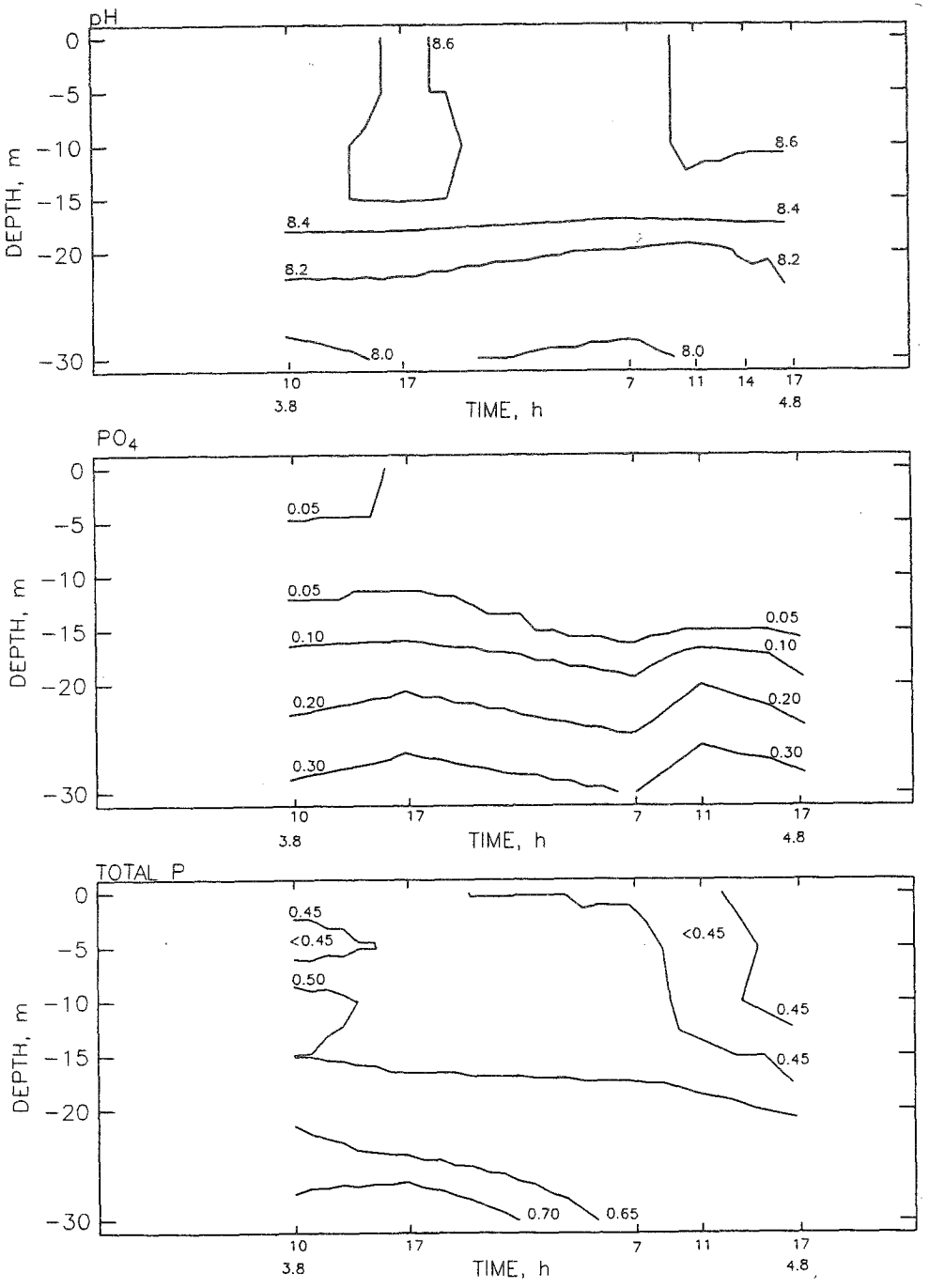


Fig. 17B. Hydrography (T ° C, S °/oo, 0_2 ml · l^{1}) pH and nutrients (NH_4-N, NO_2-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station Caliatta, August 3 - 4, 1982.

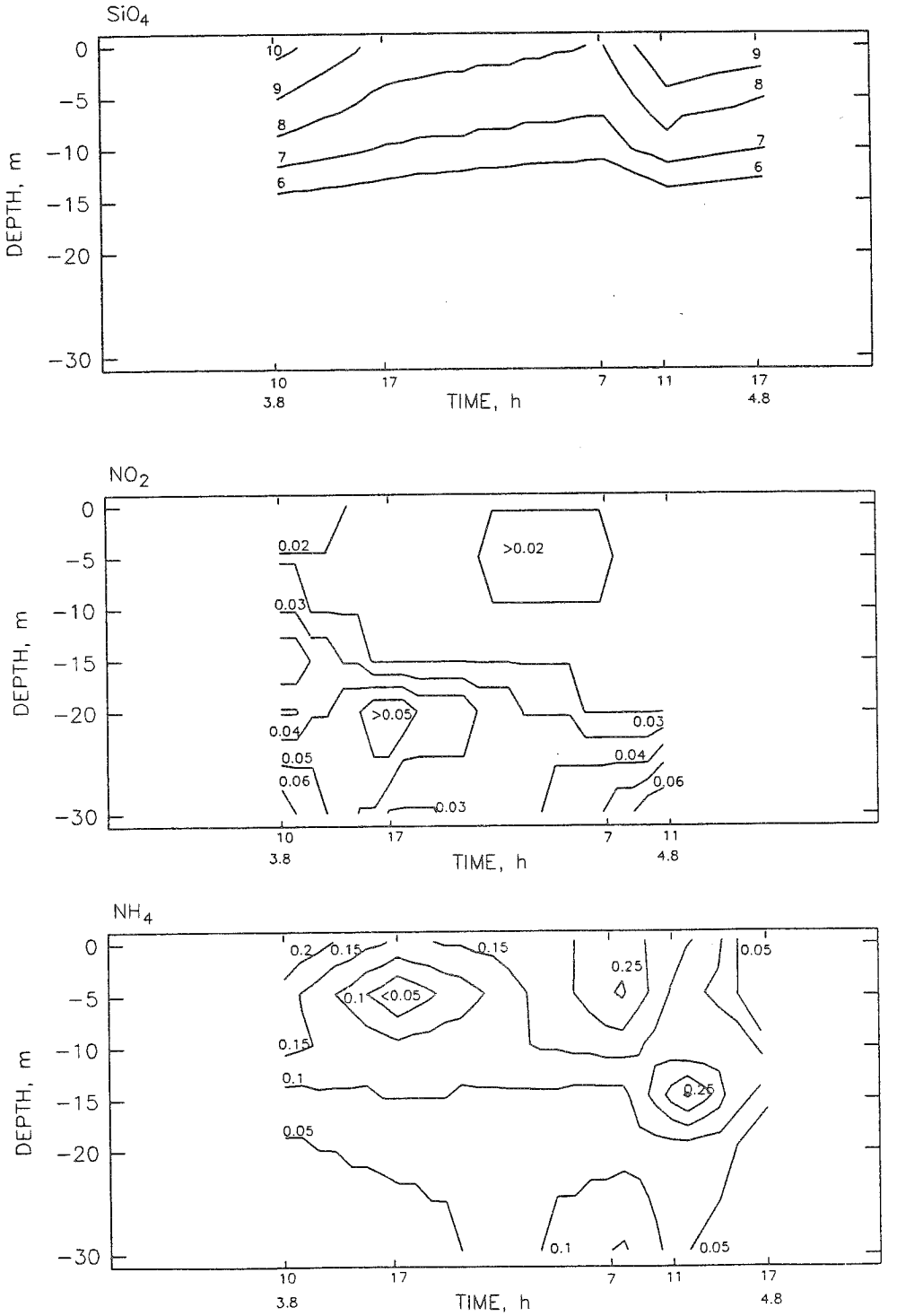


Fig. 17C. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) pH and nutrients (NH_4-N, NO_2-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station Caliatta, August 3 - 4, 1982.

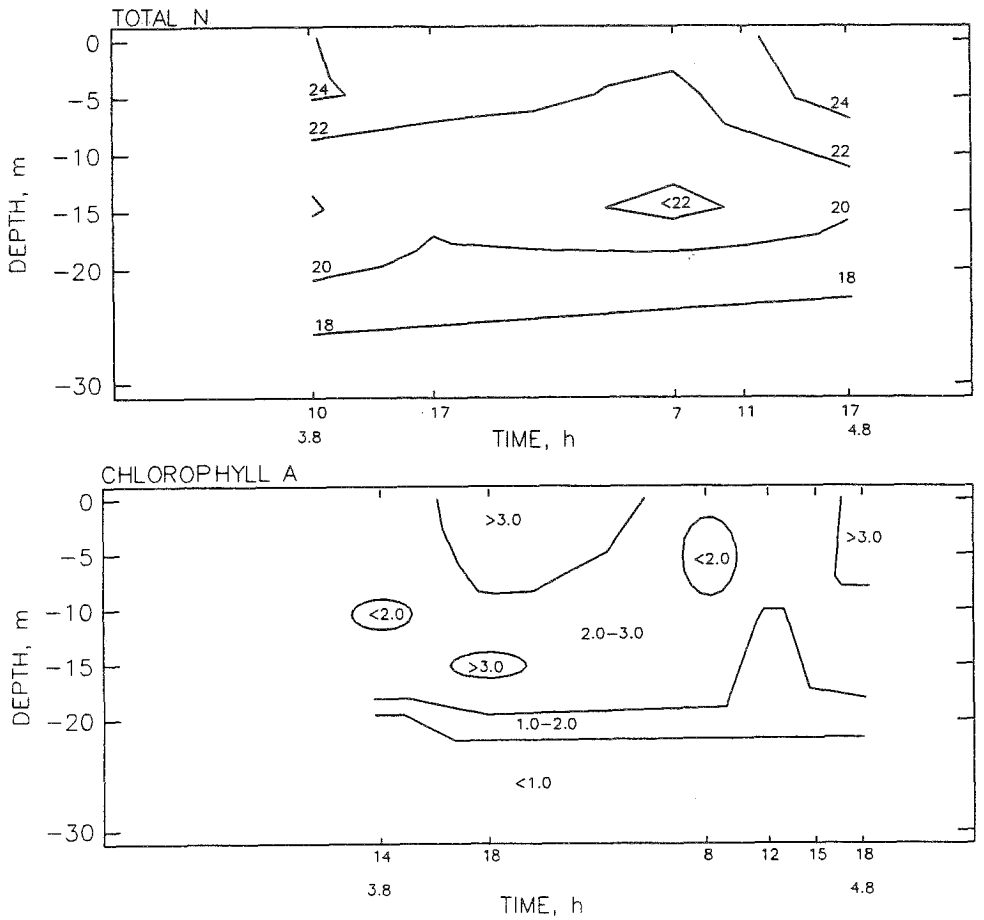
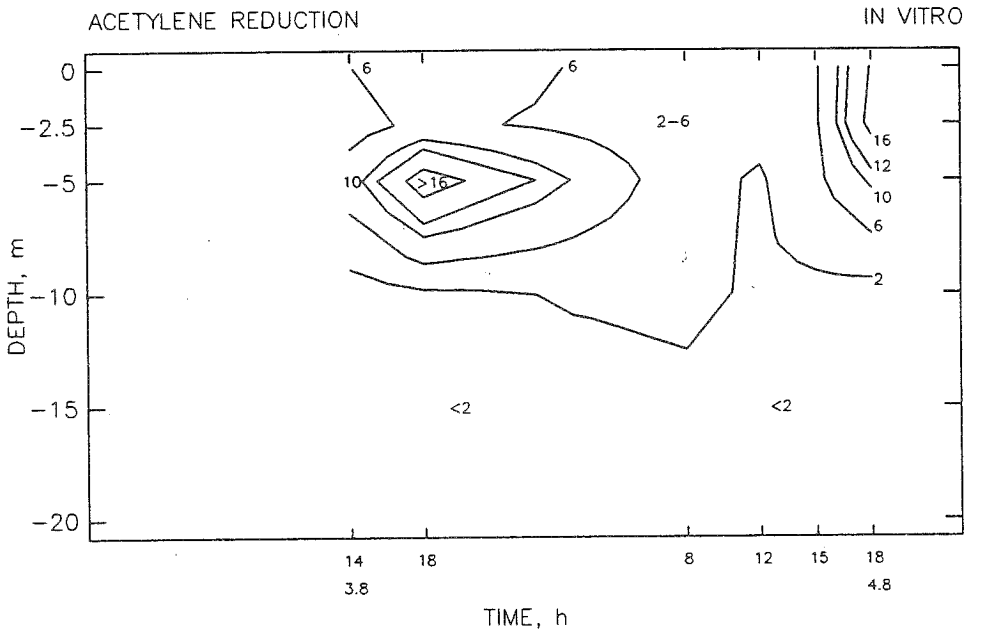


Fig. 17D. Hydrography (T °C, S °/oo, 0_2 ml · l^{-1}) pH and nutrients (NH_4-N, NO_2-N, totN, PO_4-P, totP, SiO_4-Si μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station Caliatta, August 3 - 4, 1982.



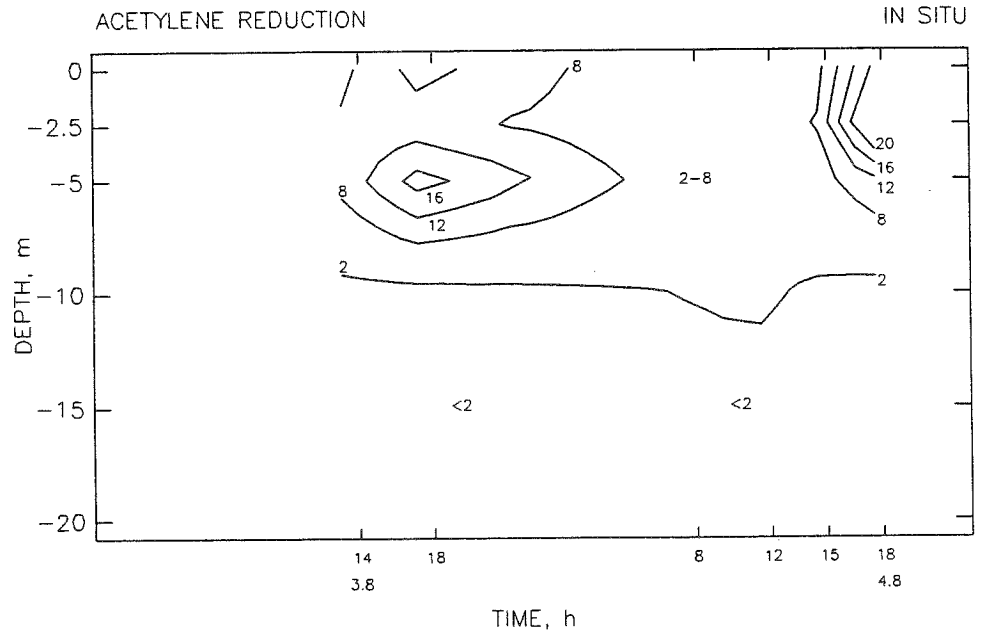


Fig. 18A. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena, Aphanizomenon flos-aquae and Anabaena spp., and acetylene reduction rate in situ and in vitro (μmol · (2 h)$^{-1}$ m^{-3}) at the anchor station Caliatta, August 3 - 4, 1982.

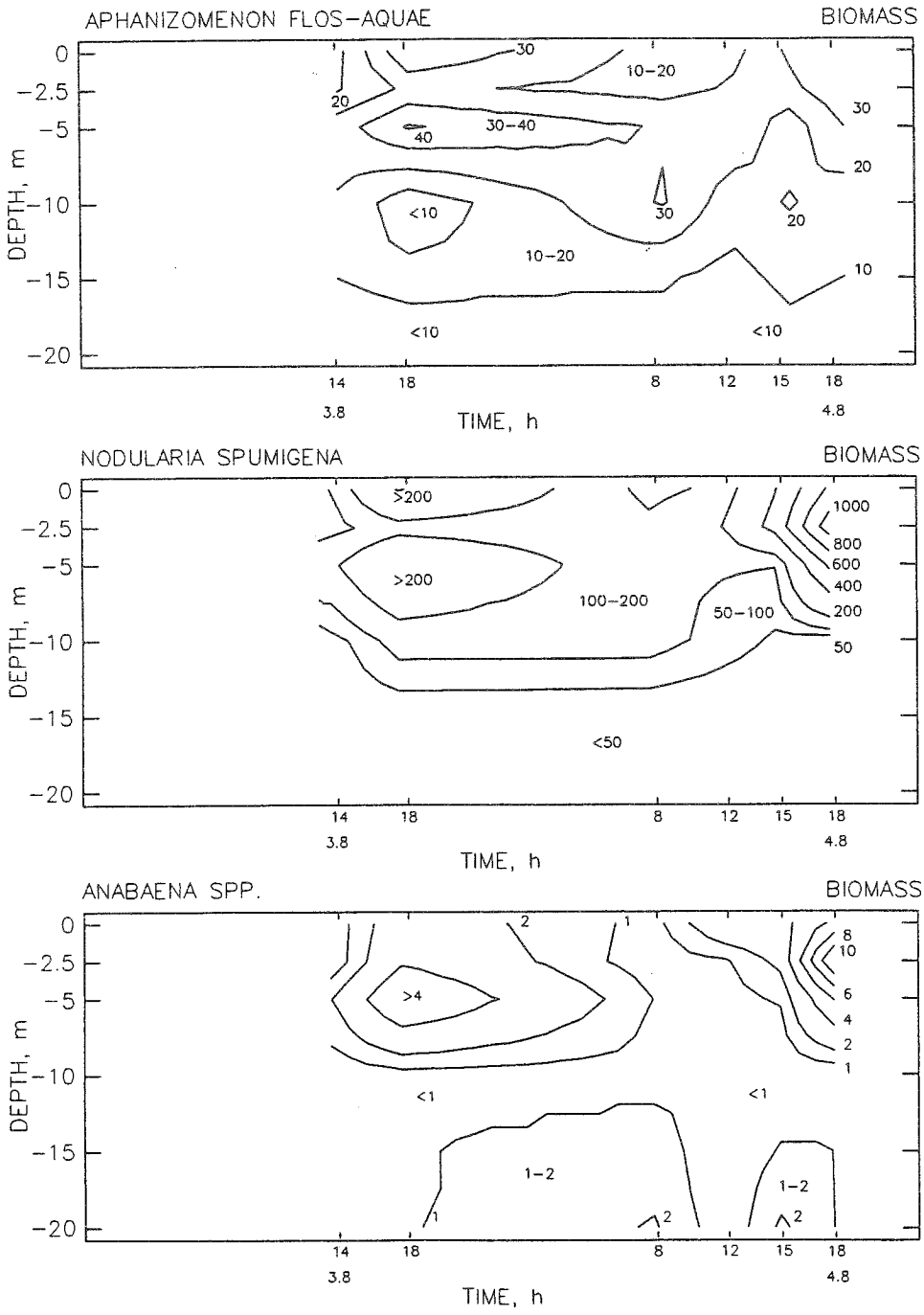


Fig. 18B. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena, Aphanizomenon flos-aquae and Anabaena spp., and acetylene reduction rate in situ and in vitro (μmol · (2 h)$^{-1}$ m^{-3}) at the anchor station Caliatta, August 3 - 4, 1982.

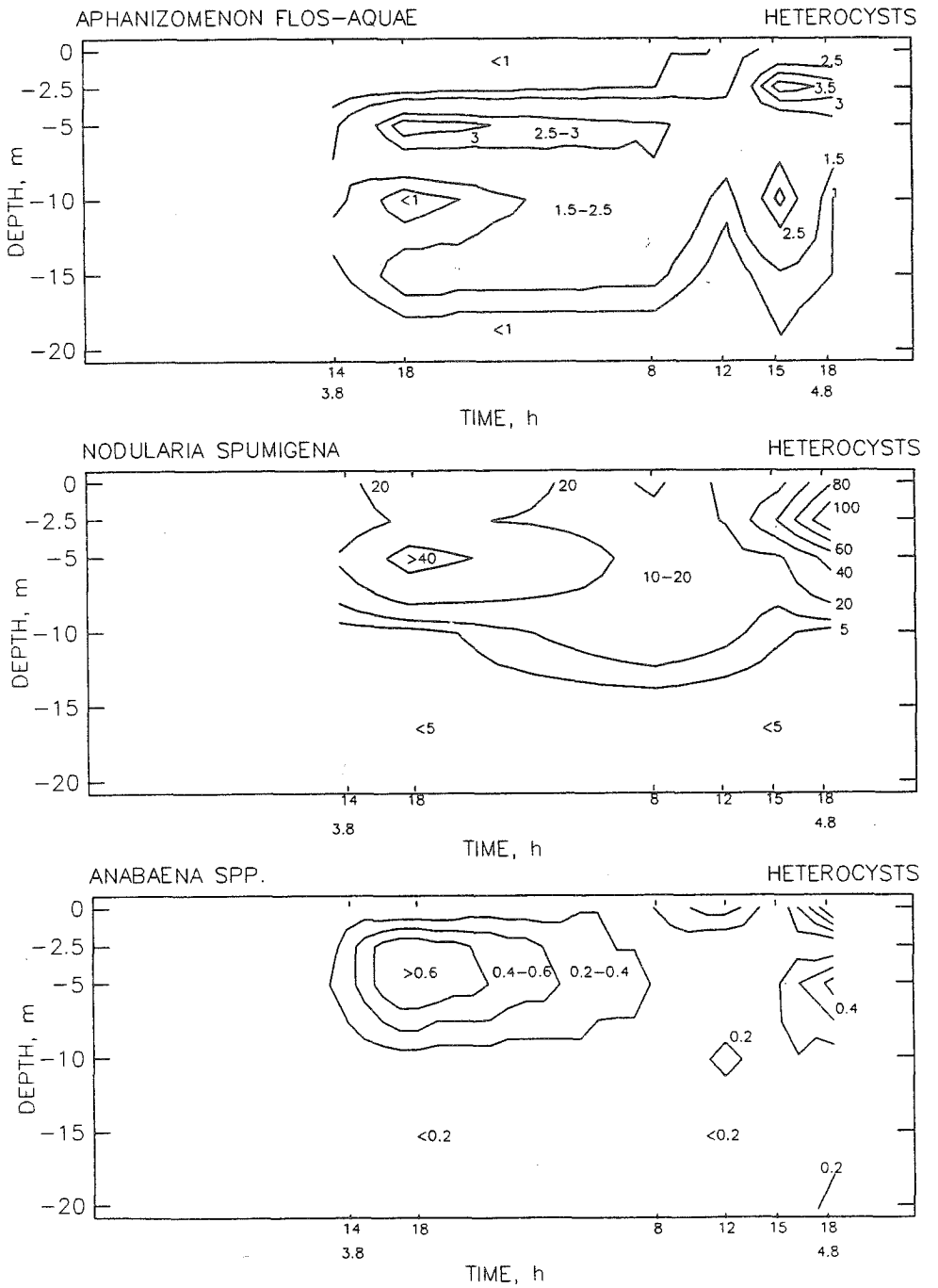


Fig. 18C. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena, Aphanizomenon flos-aquae and Anabaena spp., and acetylene reduction rate in situ and in vitro (μmol · (2 h)$^{-1}$ m^{-3}) at the anchor station Caliatta, August 3 - 4, 1982.

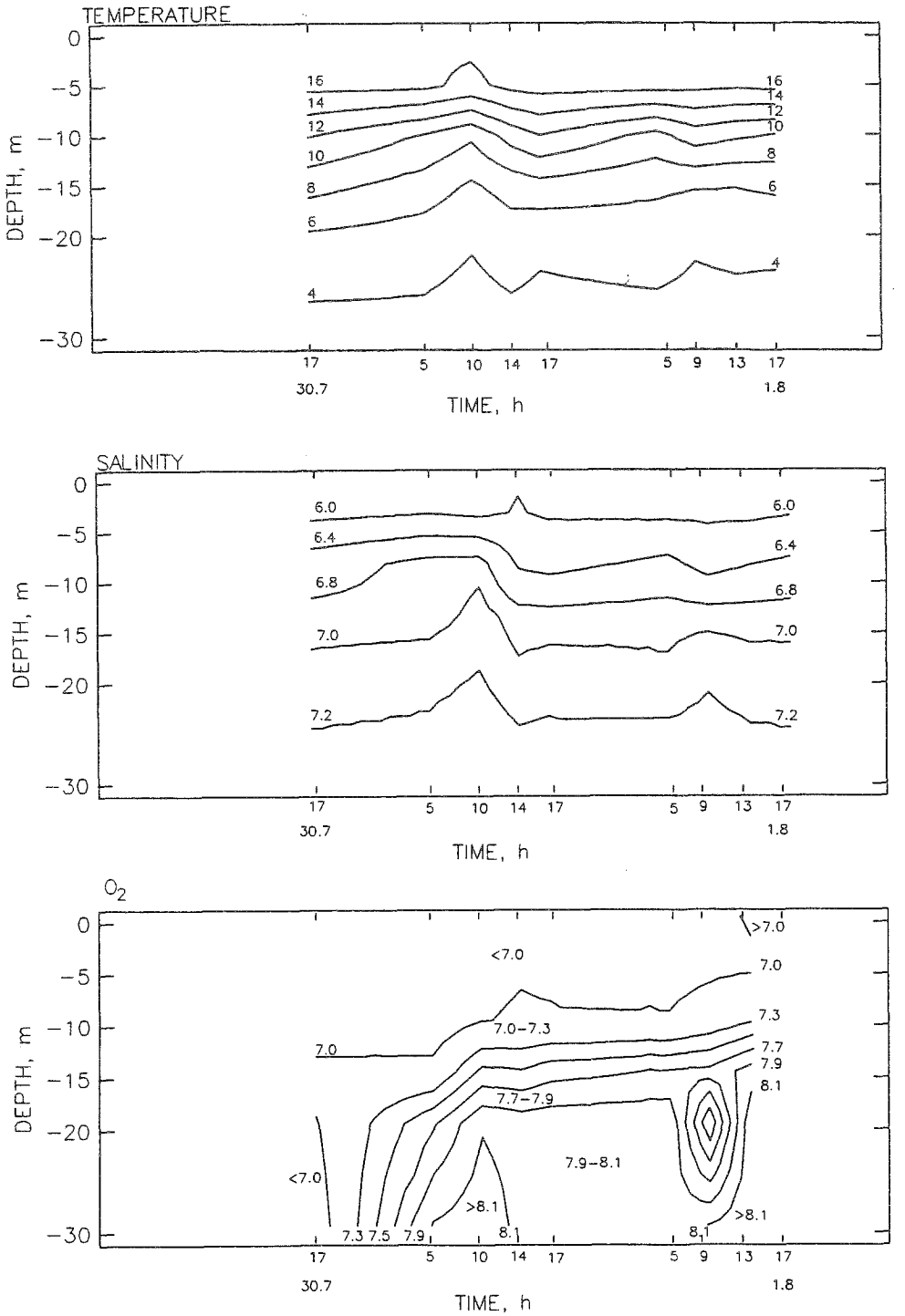


Fig. 19A. Hydrography (T ° C, S °/oo, 0_2 ml · l^{-1}), nutrients NO_3-N, NH_4-N, totN, PO_4-P, totP, μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station Ninni-84, July 30 - August 1, 1984.

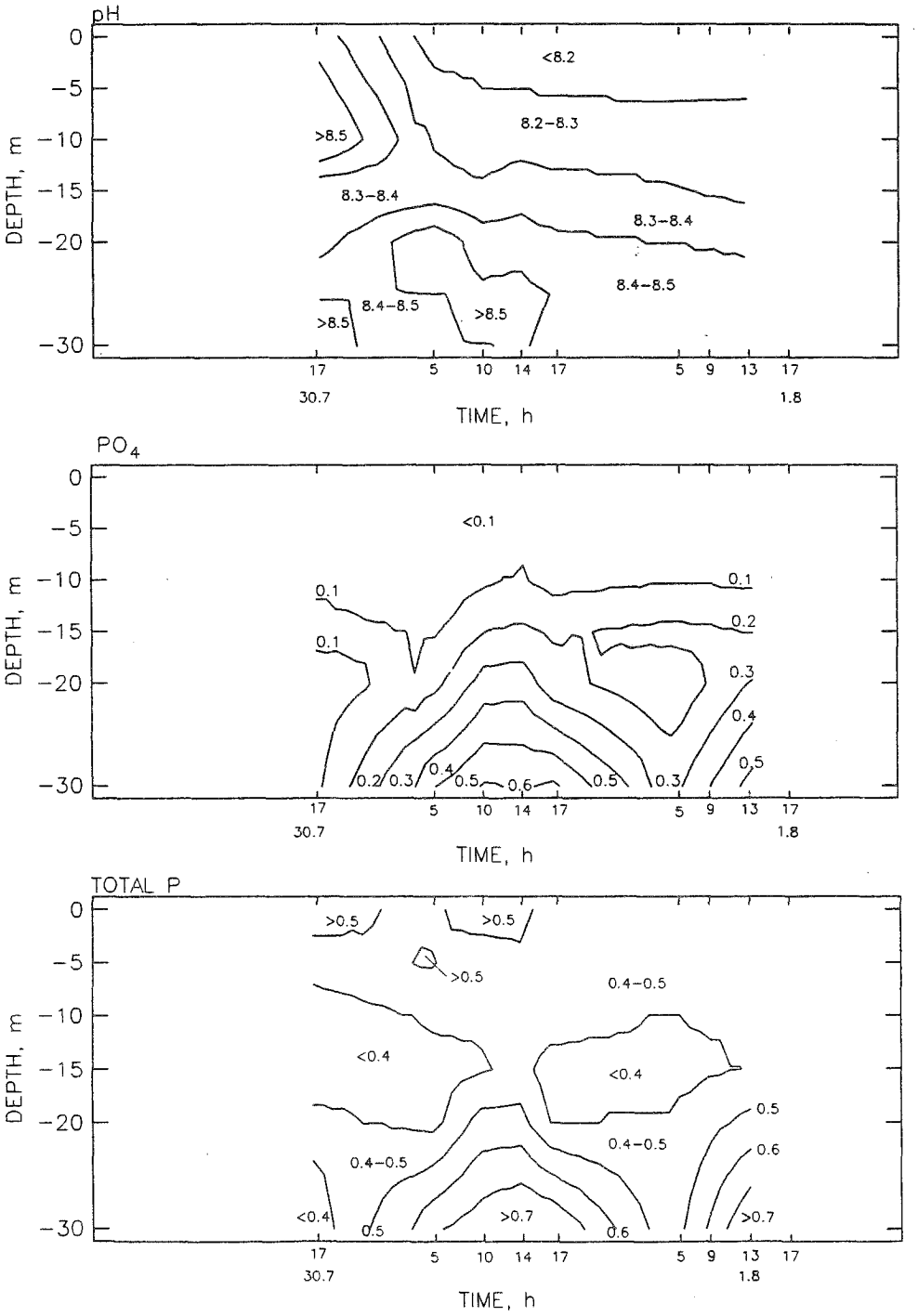


Fig. 19B. Hydrography (T ° C, S °/oo, 0_2 ml · l^{-1}), nutrients NO_3-N, NH_4-N, totN, PO_4-P, totP, μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station Ninni-84, July 30 - August 1, 1984.

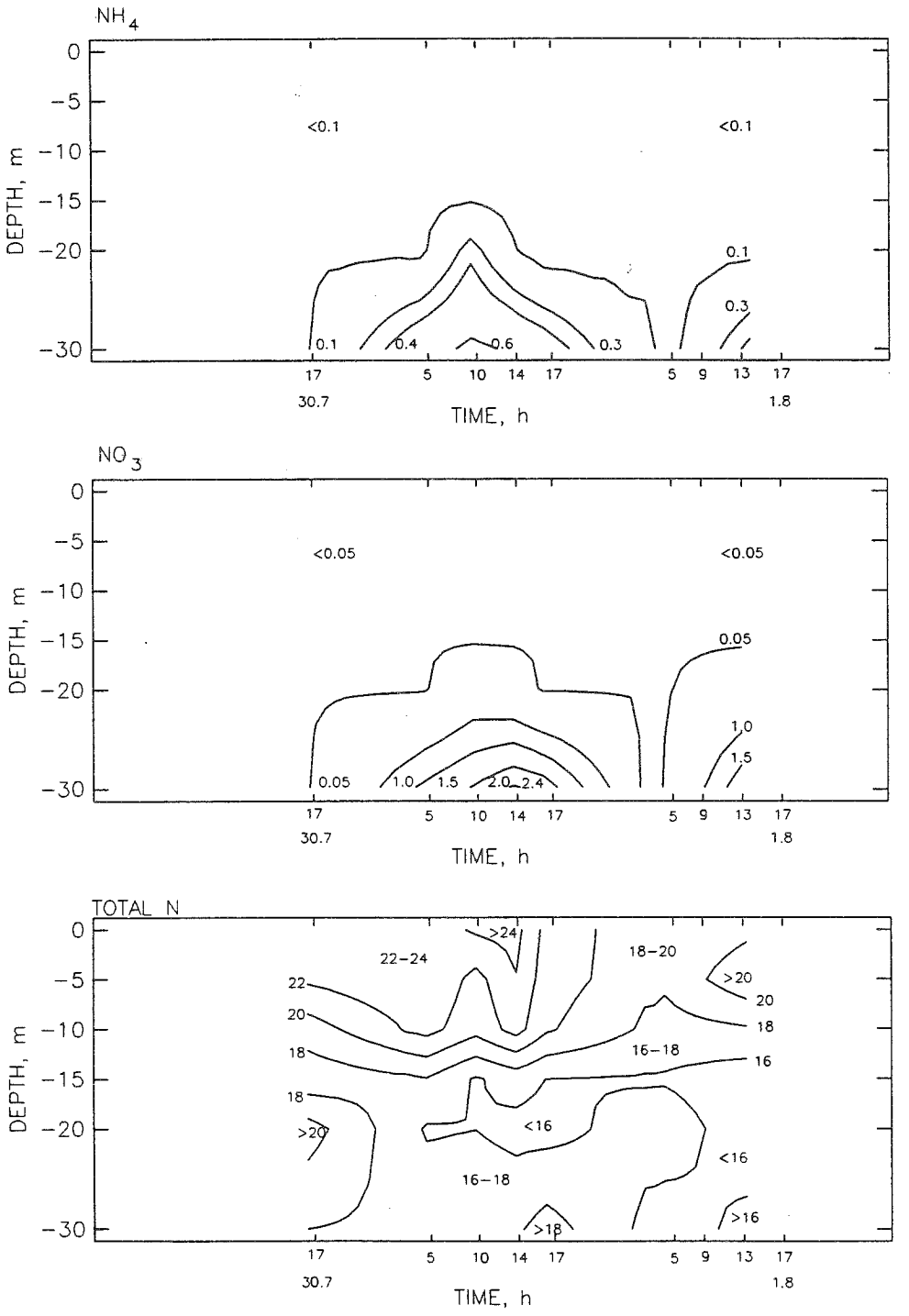


Fig. 19C. Hydrography (T ° C, S °/oo, 0_2 ml · l^{-1}), nutrients NO_3-N, NH_4-N, totN, PO_4-P, totP, μmol · l^{-1}) and chlorophyll a (μg · l^{-1}) at the anchor station Ninni-84, July 30 - August 1, 1984.

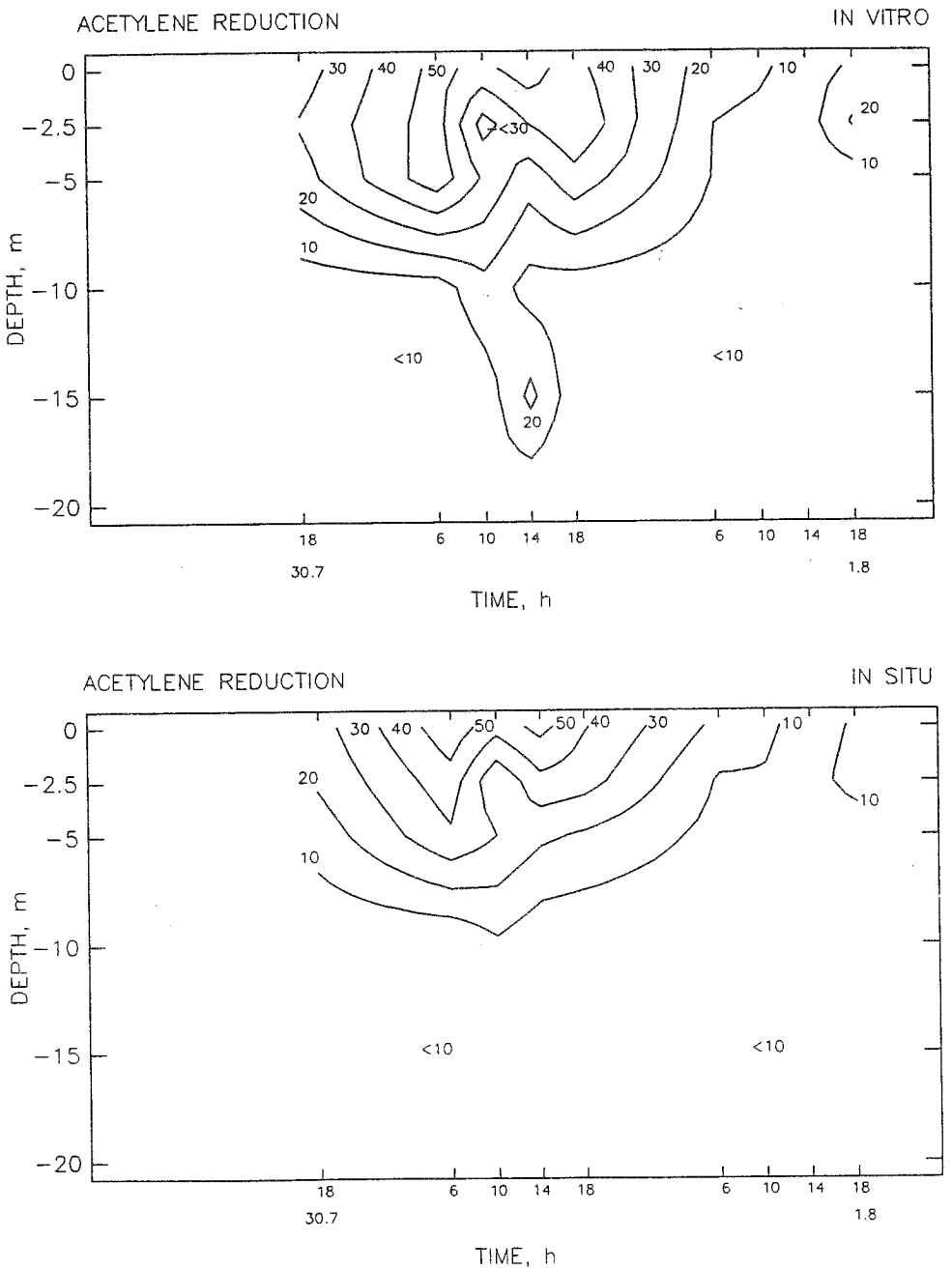


Fig. 20A. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena and Aphanizomenon flos-aquae and acetylene reduction rate in situ and in vitro (μmol (2 h)$^{-1}$ m^{-3}) at the anchor station Ninni, July 30 - August 1, 1984.

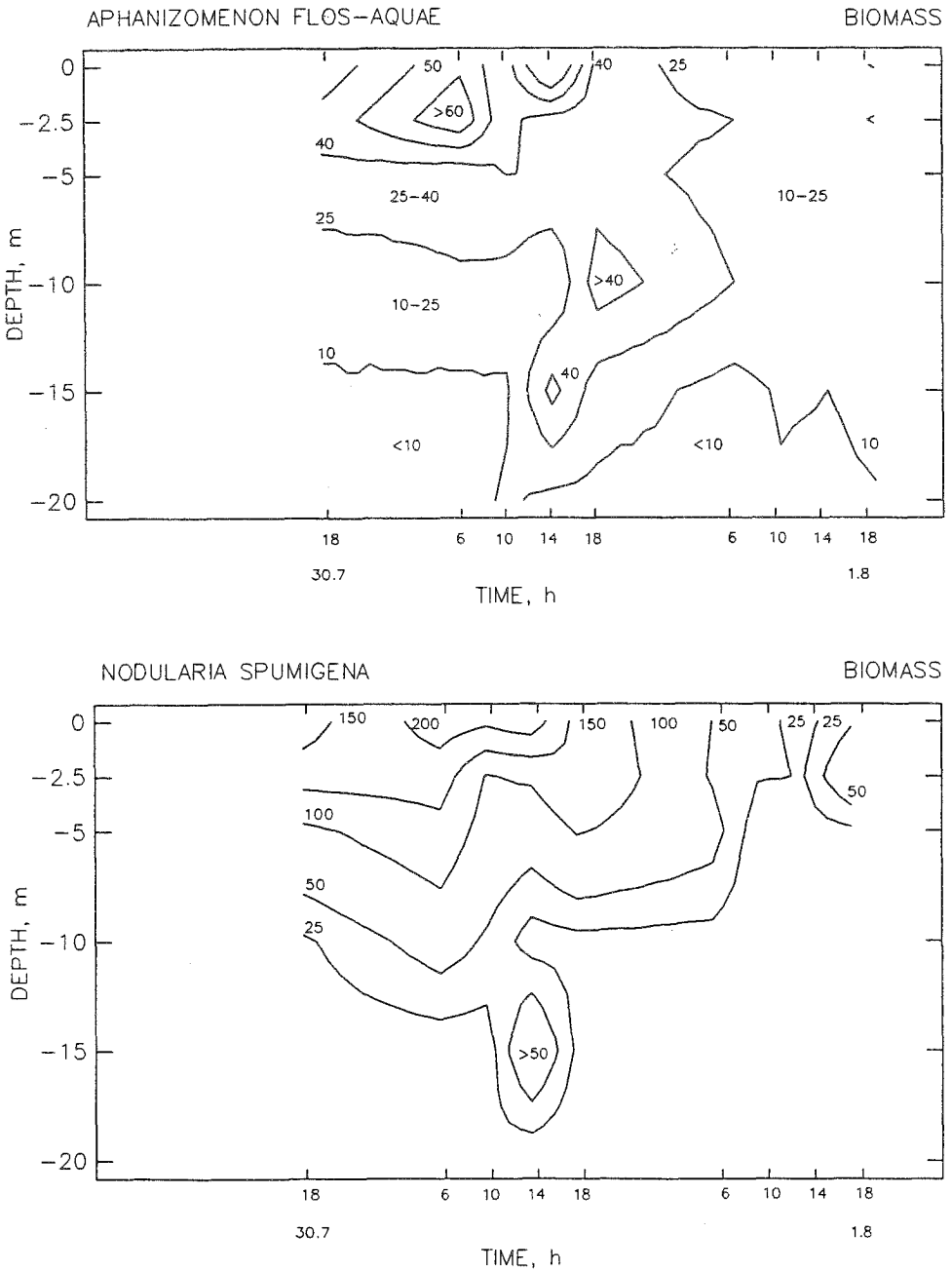
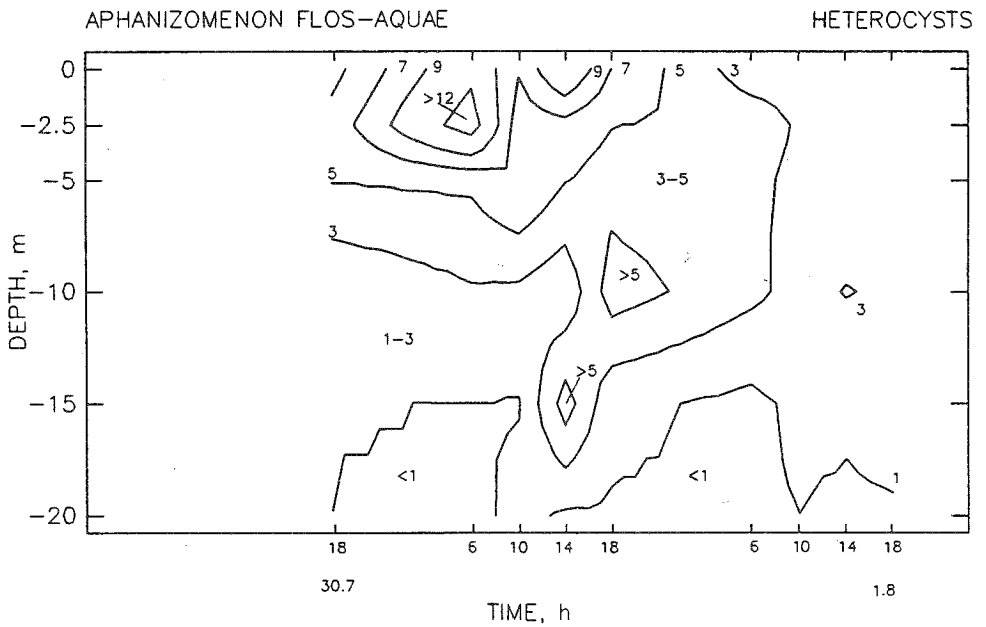


Fig. 20B. The biomass (mg $\cdot$ m^{-3}) and the number of heterocysts (10^{-6} $\cdot$ m^{-3}) of Nodularia spumigena and Aphanizomenon flos-aquae and acetylene reduction rate in situ and in vitro (μmol (2 h)$^{-1}$ m^{-3}) at the anchor station Ninni, July 30 - August 1, 1984.



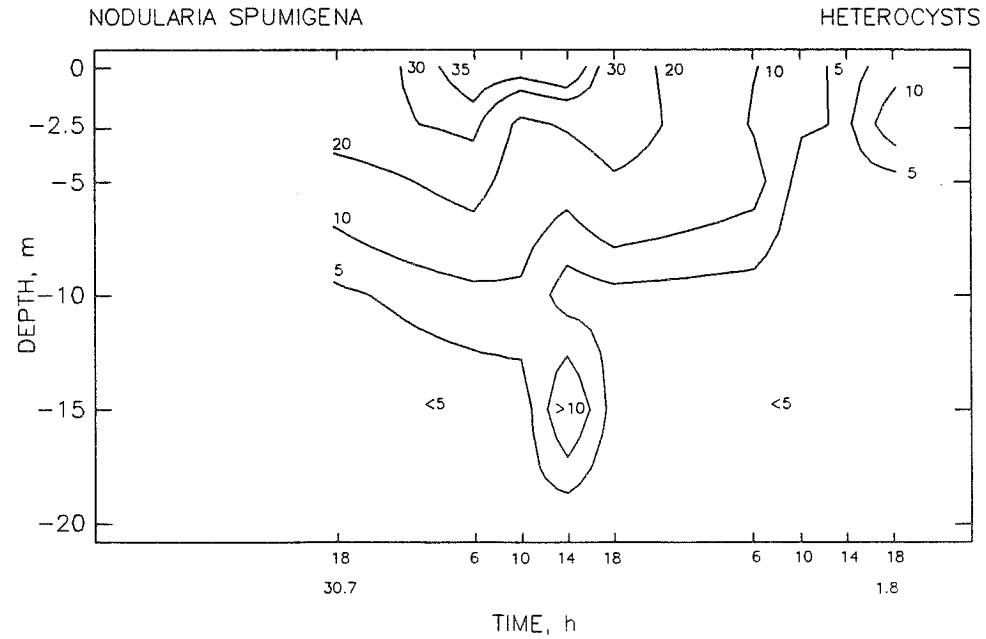
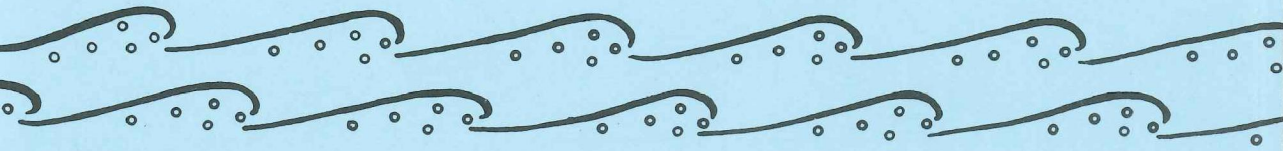


Fig. 20C. The biomass (mg · m^{-3}) and the number of heterocysts (10^{-6} · m^{-3}) of Nodularia spumigena and Aphanizomenon flos-aquae and acetylene reduction rate in situ and in vitro (μmol (2 h)$^{-1}$ m^{-3}) at the anchor station Ninni, July 30 - August 1, 1984.



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